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Cover illustration

Trollius laxus Salisb. is very rare as it nears its northeastern limit in Connecticut. Some old records indicate that it has grown in parts of New Hampshire and Maine, so it may yet be found in appropriate habitat.

Original artwork by Tess Feltes, Illustrator.

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THE TAXONOMY OF *VACCINIUM* § *OXYCOCCUS*

S. P. VANDER KLOET

In Eastern North America, both Fernald (1950) and Gleason (1952) recognized but two specific entities in *Vaccinium* § *Oxycoccus* (Hill) Koch, namely, *V. oxycoccus* L., the small cranberry and *V. macrocarpon* Aiton, the large cranberry. However, taxonomists who have dealt with the group in the boggy places of the circumboreal taiga have, as a rule, split *V. oxycoccus sensu lato* into two or more segregate species, for example, *V. oxycoccus sensu stricto* and *V. microcarpum* (Turcz ex Rupr.) Schmal. (Tutin et al., 1972); *Oxycoccus*[1] *quadripetalus* Gilib and *O. microcarpus* Turcz ex Rupr. (Bobrov & Bush, 1967); *O. microcarpus* and *O. palustris* Pers. (Polunin, 1959); *O. microcarpus, O. quadripetalus,* and *O. ovalifolius* (Michx.) Porsild (Scoggan, 1979; Porsild, 1938).

The basis for this splitting of *Vaccinium oxycoccus* s.l. into segregates stemmed from the discovery that this species is comprised of populations which have different chromosome numbers: some are diploid, 2n = 24 (Hagerup, 1940; Darrow, et al., 1944; Löve & Löve 1956; and Jorgensen, et al., 1958); others tetraploid, 2n = 48 (Hagerup, 1940; Darrow, et al., 1944; Hara, 1956; Jorgensen, et al., 1958; Löve & Löve 1966; and Pojar, 1974); and still others are hexaploid, 2n = 72 (Hagerup, 1928; Tischler, 1934; Rohweder, 1937; Newcomer, 1941; and Jorgensen, et al., 1958). However, gross morphological characters which run parallel to these ploidy levels have been difficult to find. Pedicel indumentum in conjunction with leaf dimension have been used most frequently to separate the

[1]I will not address the question of generic rank for *Oxycoccus* at this time but will follow the classification of Sleumer (1941) and Stevens (1969).

Table 1. **Comparison of morphological characters used by various authors to differentiate among the small cranberries.**

character	*taxa*			Reference
	V. oxycoccus s.s. *O. quadripetalus* *O. palustris*	*V. microcarpum* *O. microcarpus*	*O. ovalifolius*	
pedicels	pubescent	± glabrous	± glabrous	Porsild (1938)
	puberulent	glabrous		Porsild & Cody (1979)
	puberulent	glabrous		Tutin et al. (1972)
	pubescent	± glabrous		Polunin (1959)
	puberulent	usually glabrous		Ohwi (1965)
	± pubescent	glabrous		Bobrov & Bush (1967)
locations of pedicel bracts		below the middle		Porsild (1938)
	below, at, or above the middle	usually below the middle		Polunin (1959)
	near the middle	below the middle		Ohwi (1965)
	above the middle	below the middle		Bobrov & Bush (1967)
filaments	densely hairy			Bobrov & Bush (1967)
	puberulent			Tutin et al. (1972)

Table 1 (cont'd)

leaf length	6–10 mm	2–6 mm	6–8 mm	Porsild (1938)
	4–9 mm	2–4 mm		Porsild & Cody (1979)
	6–10(–15) mm	3–8 mm		Tutin et al. (1972)
	2–10 mm	2–6(–8) mm		Polunin (1959)
	5–12 mm	3–6 mm		Ohwi (1965)
	8–16 mm	3–7.5 mm		Bobrov & Bush (1967)
leaf width	2–5 mm	1.5–2 mm	2–3 mm	Porsild (1938)
	3–6 mm	1–2.5 mm		Tutin et al. (1972)
	1.5–5 mm	1–2(–3) mm		Polunin (1959)
		2–2.5 mm		Ohwi (1965)
	3–6 mm	1–2.5 mm		Bobrov & Bush (1967)
berry diameter	8–12 mm	5–7 mm	10–12 mm	Porsild (1938)
	8–14 mm	5–10 mm		Porsild & Cody (1979)
	(6)8–10(–15) mm	5–8 mm		Tutin et al. (1972)
	7–13 mm	5–7(–8) mm		Polunin (1959)
	10 mm	6–7 mm		Ohwi (1965)
	10–18 mm	5–10 mm		Bobrov & Bush (1967)
chromosome number	2n = 48	2n = 24		Tutin et al. (1972)
	2n = 48	2n = 24	2n = 48	Darrow et al. (1944)

diploid *V. microcarpum* from the tetraploid *V. oxycoccus* s.s. (Table 1). The hexaploids (2n = 72) occur infrequently and are thought to be sterile hybrids between *V. oxycoccus* and *V. microcarpum* (Hagerup, 1940; Camp, 1944). But as Table 1 shows, these characters (as interpreted by the various authors) do not unerringly separate the diploids from the tetraploids nor are pedicel indumentum and leaf dimensions invariably correlated: there are plants with glabrous pedicels which have the leaf size of *V. oxycoccus* s.s. and these have been referred by Porsild (1938) to *O. ovalifolius;* and then there are those plants which have pubescent pedicels and very small inrolled leaves and which have been referred to *O. palustris* ssp. *microphyllus* (Lge.) Löve & Löve, or by Camp (1944) to the "microcarpoid" phase of *O. quadripetalus.*

In her study on the variability of several vegetative and inflorescence characters in 50 *Vaccinium oxycoccus* specimens gathered from six bogs near Durham, New Hampshire, Rodrigues (1963) found that stem color varied from light brown to black; that leaf width varied from 1 to 4 mm and length varied from 3 to 10 mm and had mean dimensions of 2 ± 0.5 mm $\times$ 6 ± 1 mm which is interesting insofar as these values fall just at the boundary between Porsild's (1938) concept of *V. microcarpum* and *V. oxycoccus* (see table 1); that the leaf blades of several specimens were flat, others slightly revolute, and yet others revolute (conditions she attributed to relative exposure of the plants); and that the leaf apices were mostly pointed and that only a few had slightly rounded apices. She also showed that a significant source of the leaf variation described above arose from between plants rather than within plants.

Furthermore, Rodrigues (1963) described all the pedicels as pubescent, bearing a pair of green or red bracts (a few pedicels had none at all) whose shape varied from long and narrow to leaf-like to very small scales. Pedicel number varied from one to four and in 21 specimens arose from the axils of the uppermost reduced leaves, thereby forming an apparent terminal cluster (figure 1); in the remainder, however, the pedicels were in the axils of the lowermost reduced leaves of a normal leafy branch: a condition I have also observed in Cape Breton, Nova Scotia (figure 8) and which results in an inflorescence type usually associated with *Vaccinium macrocarpon.*

Indeed, as Boivin (1967) has noted, "the diagnostic characters [for the small cranberry taxa] are not quite constant and various recom-

binations of characters occur here and there. He who would here accept two species will eventually be led to accept four, then perhaps eventually eight. . . !"

Another difficulty arises whenever herbarium specimens are examined. A sheet of several fragments (see figures 1, 2, 3, especially their annotations) each bearing one or two pedicels, several of which may be quite glabrous, others quite puberulent, may be the result of a mixed gathering; a likely event since, according to Bobrov & Bush (1967) *Oxycoccus microcarpus* often occurs with *O. quadripetalus* in boreal peat bogs.

Nonetheless Camp (1944) argued that diploid *Vaccinium microcarpum,* which is found in Iceland, Europe, Asia, and northwestern North America but is unknown from Labrador and Greenland, is quite homogeneous and is distributionally disjunct from its sister group *V. macrocarpon.*

Furthermore, according to Camp (1944) *Oxycoccus quadripetalus* is a mixture of tetraploid hybrids and their segregates which resulted from the contact *O. microcarpus* made with *V. macrocarpon* when it migrated southward in response to the advancing Pleistocene ice sheets.

The purpose of this paper is to test Camp's hypothesis, that in *Vaccinium* § *Oxycoccus* there are in fact two rather homogeneous diploid taxa, *V. macrocarpum* and *V. microcarpum* respectively, and a tetraploid-hexaploid population comprising a heterogeneous assemblage of hybrids and their segregates, using numerical and experimental taxonomic techniques.

MATERIALS AND METHODS

To assess morphological discontinuity 26 likely cranberry habitats, mostly in eastern North America, such as bogs, raised bogs, boggy barrens, high moors, wet meadows, headlands, and low tundras were surveyed between 1969 and 1980 (for geographical details see Appendix). If, after a careful search, a site had more than ten cranberry colonies present, three 200 m grid lines were laid out in a random fashion. At every 10 m, the nearest cranberry plant was flagged and identified by number. If there was no plant within 1 m of the 10-m mark of the tape, the point was declared empty. For every 10 plants flagged, three were drawn at random and permanently tagged so that they could be revisited during the flowering

FISHER SCIENTIFIC
PLANTS OF ALASKA (1)
Common in open areas in Sphagnus bog.
Sterling Highway between Kasilof and Homer, Kenai Peninsula,
No.5417 J.A.Calder June 24 1951
DIVISION OF BOTANY, SCIENCE SERVICE
DEPARTMENT OF AGRICULTURE, OTTAWA, CANADA

Figure 1. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

Figure 2. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

Figure 3. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

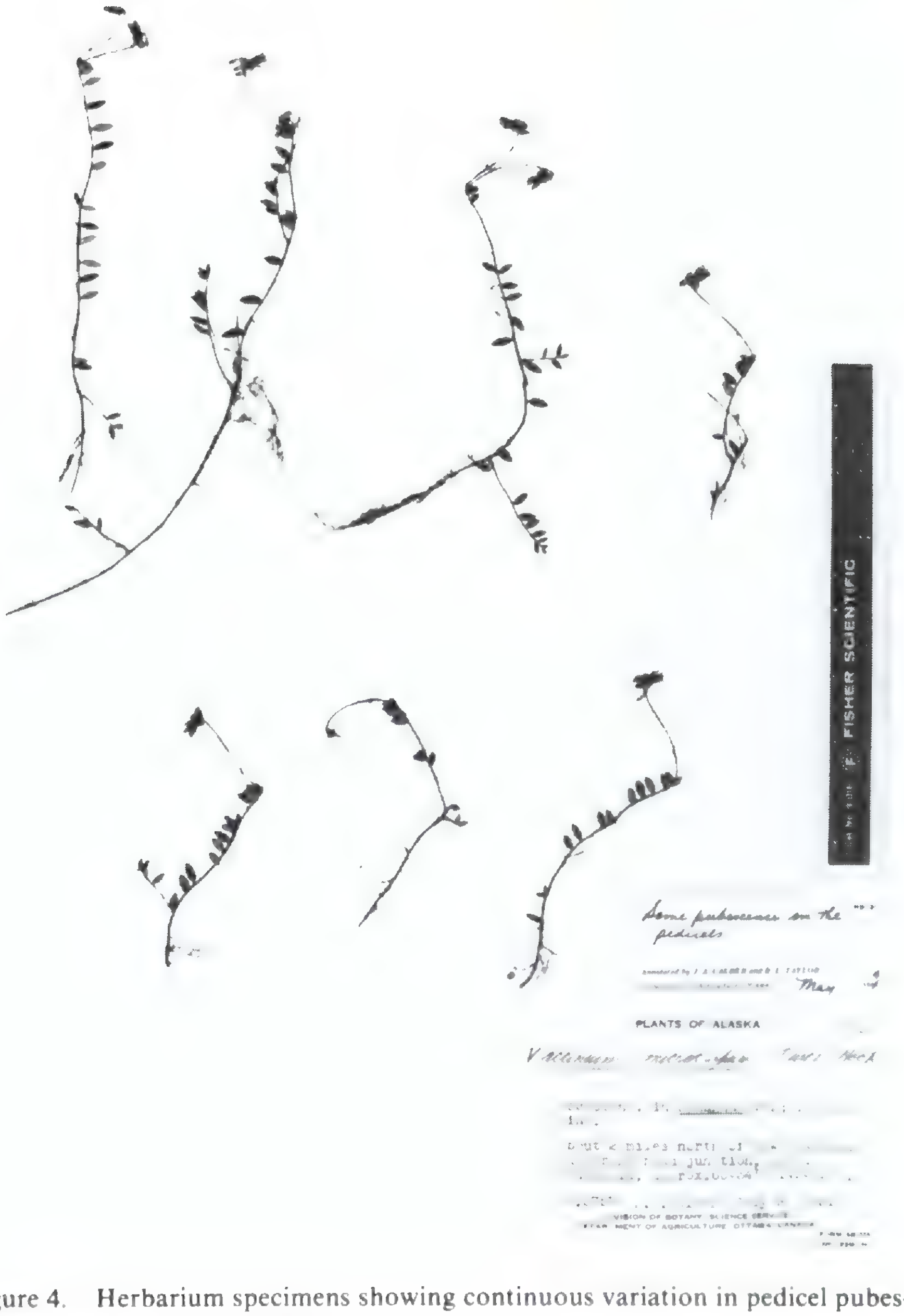


Figure 4. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

Figure 5. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

Figure 6. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

Figure 7. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

and fruiting season for at least two reproductive bouts. Flowers, fruits and a few mature vines from each number were collected and dried. Voucher specimens are at ACAD[2]. Soil samples were taken and ecological habitat notes were made for each collection. In addition, a few, usually five or more, berries were harvested from each plant so that germination trials could be carried out and the growth morphology of the seedlings compared with that of the female parent.

Table 2. **Morphological comparison between selected attributes of *V. macrocarpon* and *V. oxycoccus***

character	*V. macrocarpon* (n = 136)	*V. oxycoccus* (n = 246)
length of flowering shoot (cm)	5.5 ± 3.4	2.3 ± 0.8
width of pedicel bracts (mm)	1.3 ± 0.4	0.4 ± 0.2
leaf width (mm)	3 ± 0.5	2 ± 0.7
leaf length (mm)	8 ± 1.3	5 ± 1.5
ratio w:l	1:2.66	1:2.50
leaf shape	narrowly elliptic	ovate
berry diameter (mm)	12 ± 2	9 ± 2
large seeds/berry	17 ± 8	8 ± 5
seed weight (mg/100)	91 ± 28	68 ± 17

Next, 114 dried specimens were scored for the following 12 features: (1) length of fertile shoot; (2) width of bracts on pedicel at anthesis; (3) pedicel indumentum (pubescent, intermediate, or glabrous); (4) calyx lobes (pubescent at the tip or glabrous); (5) stamen filaments (pubescent, pubescent along the margins, or glabrous); (6) leaf blade (revolute, intermediate, or flat); (7) mean leaf width; (8) mean leaf length; (9) leaf length to width ratio; (10) leaf shape (ovate, narrowly ovate, or narrowly elliptic); (11) indumentum in

[2]Acronyms follow *Index Herbariorum* (Holmgren & Keuken, 1974).

twigs of the current season (puberulent or glabrous); (12) berry diameter.

However, since my sampling space was restricted to northeastern North America, where according to Camp (1944) and Porsild (1938) *V. microcarpum* is absent, I decided to augment the basic data matrix described above with selected herbarium specimens (cited under specimens examined) from the Northwest Territories where according to Porsild & Cody (1979) *V. microcarpum* is frequent and *V. oxycoccus* is rare, known to occur only from a few muskegs adjacent to the Liard and upper Mackenzie Rivers.

Furthermore, because my sampling procedure was unbiased towards the inclusion of rare "morphs", I also added several herbarium specimens which had been identified as *Vaccinium oxycoccus* var. *microphyllum* or *V. oxycoccus* var. *intermedium* or *V. oxycoccus* var. *ovalifolium* or looked somewhat dubious.

Whenever a herbarium specimen had a missing feature (e.g. no ripe berries) I would dub in the appropriate value using the Flora of the region where the plant had been collected: thus if fruit was absent from a Keewatin specimen which had been referred to *V. microcarpum*, I would check Porsild & Cody (1979) for berry size and use their median value for the data matrix.

After the discretely scored characters had been converted to multistate characters, a non-metric coefficient $S_{SM} = \frac{M}{m+u}$ was calculated for each pair of specimens; then the similarity coefficients were sorted by way of an unweighted pair-group clustering method based on arithmetic averages (UPGMA). Sneath & Sokal (1973, p. 132 & p. 230) furnish details of these procedures.

Since dendrograms are only useful at depicting nearest neighbour relationship and are less reliable at the higher internodes, i.e. at the group level, I also subjected the data matrix to Principal Component Analysis. In this procedure individuals are ordered along uncorrelated axes, while variation in all characters among all the individuals is considered simultaneously (Sneath & Sokal, 1973, pp 245-247). Any major groupings in the sample data are elucidated through this sorting technique. In summary then, UPGMA is very useful in describing the relationship between pairs of individuals, while PCA detects major patterns in the data.

For the actual processing, I used the numerical taxonomy system (NT-SYS) written by F. J. Rohlf, J. Kishpaugh and D. Kirk (1974,

Figure 8. *V. oxycoccus* bearing a "normal" flowering shoot *(Vander Kloet 419673)*.

State University of New York, Stony Brook). In the PCA routine, however, the character states were not converted to multistate characters but were read as continuous, which is justifiable since all the characters scored were ordered.

Once the germinated seedlings had had their chilling requirements fulfilled in a cold frame, and had begun to produce new shoots and/or flower buds, several actively growing stem tips or developing floral primordia were fixed, stained, and squashed according to a procedure described by Hall & Galletta (1971) so that the chromosome number for a number of plants might be ascertained.

Finally, to substantiate distribution data, herbarium specimens from North America were examined at A, ACAD, ALTA, BM, CAN, DAO, GH, K, LINN, NEBC, NHA, NY, NYS, PH, QK, TRT, UAC, UBC, and V.

RESULTS

In the first dendrogram (figure 9), which is based on field data only, initial separation occurred at a similarity coefficient of 0.38 and resulted in the formation of two groups: one whose members fell within the circumscription of *Vaccinium macrocarpon* and the other *V. oxycoccus* sensu Fernald (1902 & 1950) and Rodrigues (1963). Inspection of some of the smaller clusters within these specific groups shows that the *V. macrocarpon* cluster contains more variability than the *V. oxycoccus*. Thus OTU's 68, 57, 75, 69, 63 and 66 form a subgroup of ± glabrous members in *V. macrocarpon*, whilst OTU's 79, 54, 82, 71, 81, 78, 55, 62, 58, and 65 form a subgroup of rather robust and pubescent plants.

When the herbarium specimens were added to the matrix, initial separation occurred at a similarity coefficient of 0.35 (figure 10) and again resulted in the formation of two groups, namely *Vaccinium macrocarpon* and *V. oxycoccus* s.l. OTU 10 was the only specimen added to the *V. macrocarpon* cluster; this specimen had been misidentified as *V. oxycoccus*. Within the *V. oxycoccus* cluster several new groups appeared: the most noteworthy of these being OTU 6, a specimen which can be referred to *Oxycoccus ovalifolius* since it has glabrous pedicels and large flat ovate leaves, and OTUs 2, 3, 44, 9, and 43, a mixture of specimens which had been identified as *V. microcarpum* and *V. oxycoccus* var. *microphyllum*.

The remaining *V. oxycoccus* var. *microphyllum* specimens (OTU's 45, 42, 46, 41, 47, and 7) were linked more closely to *V. oxycoccus* per se.

Table 3. **Difference in germination of autumnal and vernal collections of *Vaccinium* § *Oxycoccus* seeds.**

Collection Time	taxa	samples	number of seeds	% germination	Radicle emerges days	Dicotyledons days	True leaves days
Autumnal harvest	*V. oxycoccus*	19	1067	21	19 ± 4	30 ± 3	38 ± 7
	V. macrocarpon	17	2434	5	26 ± 10	38 ± 12	47 ± 14
Vernal harvest	*V. oxycoccus*	18	1057	92	10 ± 2	19 ± 1	24 ± 3
	V. macrocarpon	19	2082	52	9 ± 1	19 ± 2	25 ± 2

Note: ± = one standard deviation.

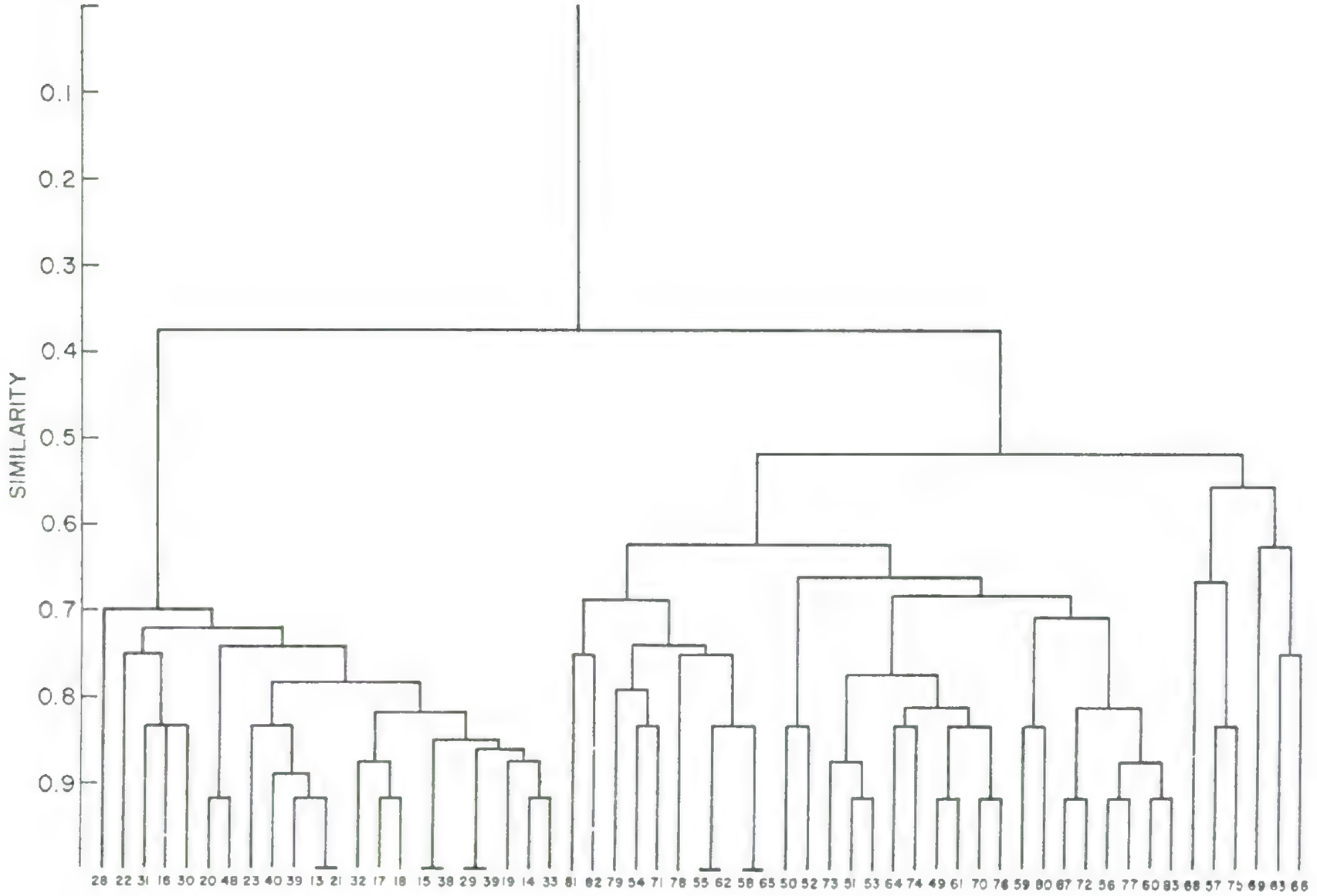


Figure 9. Dendrogram depicting relationships among 57 OTU's of *Vaccinium* § *Oxycoccus* specimens from 25 collecting sites in North America. (Details in text.)

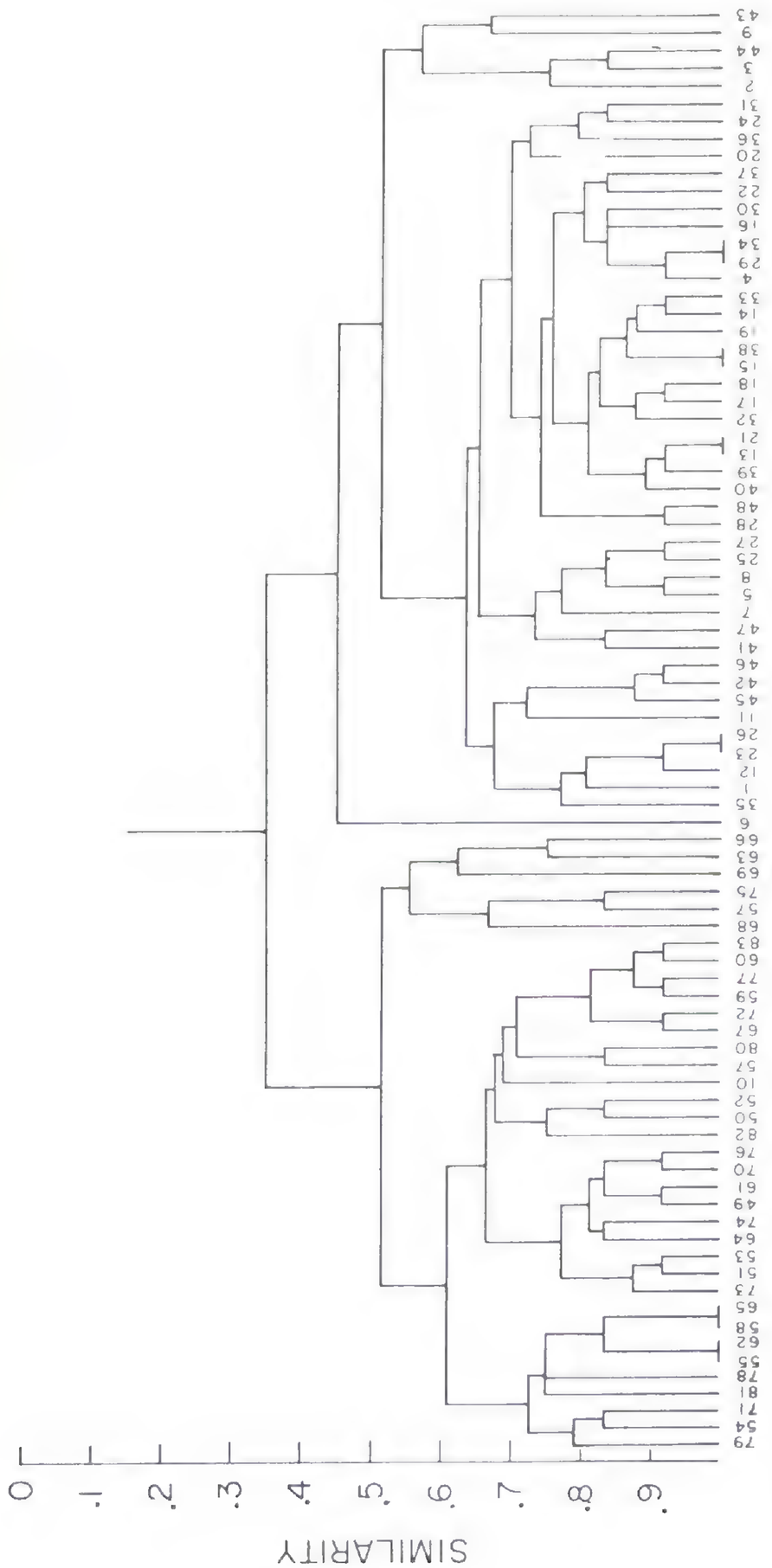


Figure 10. Dendrogram depicting relationships among 83 OTU's of *Vaccinium* § *Oxycoccus* based on both field and herbaria collections. (Details in text.)

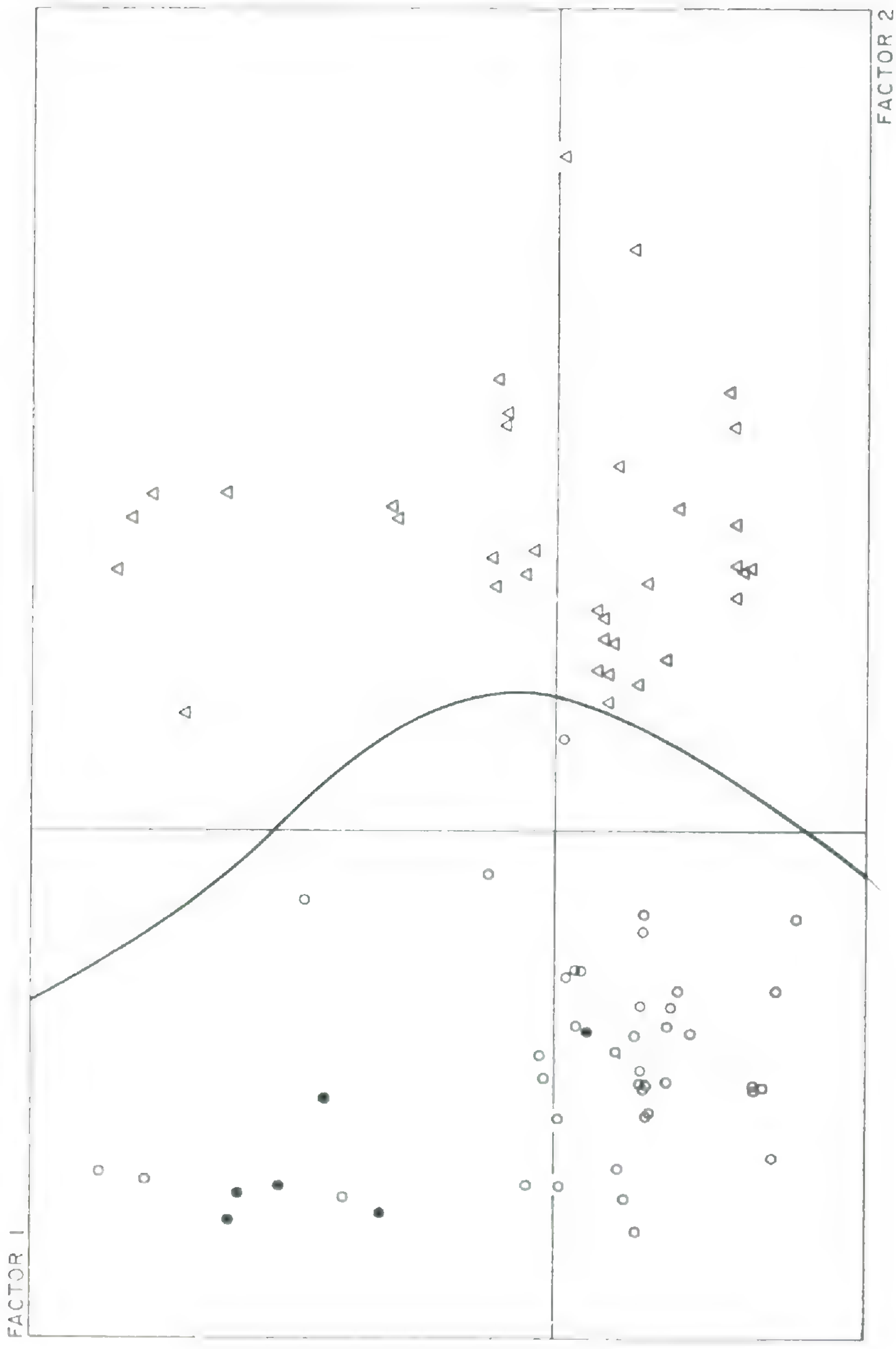


Figure 11. Principal Component Analysis. Projection of the first two factors. (Details in text.) *Vaccinium oxycoccus* on concave side of curve, *V. macrocarpon* outside curve. Triangles — *V. macrocarpon;* Open circles — *V. oxycoccus* s.s.; Closed circles — *"V. microcarpum"*.

In the Principal Component Analysis (figure 11), the first two factors accounted for 64% of the variance. Two major clusters were delimited: *Vaccinium macrocarpon* and *V. oxycoccus* s.l. respectively. In the *V. oxycoccus* cluster OTU 6 (a specimen which had been identified as *V. oxycoccus* var. *intermedium*) occupies an isolated position. The specimens identified as *V. microcarpus* and *V. oxycoccus* var. *microphyllum* are again confounded and form (with the exception of OTU 47) a loose aggregate distinctly separated from the central constellation. Similarly, in the *V. macrocarpon* group the ± glabrous plants occupy a somewhat isolated position.

In short, the numerical analyses suggest that the *Vaccinium macrocarpon* cluster contains as much variability as the *V. oxycoccus* group; they do not lend support to the notion that *V. oxycoccus* s.l. contains discrete morphological taxa that reflect ploidy level. Furthermore, at the phenetic level at least, Camp's (1944) hypothesis that *V. macrocarpon* and *V. microcarpum* are relatively homogeneous taxa (i.e. contain relatively little variability) and that *V. oxycoccus* s.s. is a heterogeneous assemblage could not be substantiated.

To recognize the "microcarpus-microphyllus" group isolated in the Principal Component Analysis as a separate taxon would confuse the very issue it was designed to clarify: that the tiny leaved, largely glabrous, diploid populations in *Vaccinium oxycoccus* s.l. are morphologically distinct from the tiny leaved, somewhat puberulent, tetraploid populations. Moreover any major herbarium holding will have sufficient specimens on hand so that a continuous series from the very small delicate plants to those which are quite robust can be compiled (figures 1-7). However, plants at either end of this morphological spectrum are much more common in the herbaria than in the field.

Mixed gatherings on a single herbarium sheet occur (figure 12), but this condition is usually readily identifiable using uniformity of leaf size and shape as a guide. Therefore specimens such as in figures 1-4 are most likely single gatherings which exhibit variability in pedicel indumentum, thereby indicating that perhaps pedicel indumentum is an unreliable diagnostic feature.

Furthermore, although much has been made of inrolled leaves in *Vaccinium oxycoccus* in both descriptions and diagnostic keys, this feature, as Rodrigues (1963) has implied, is quite plastic. I have

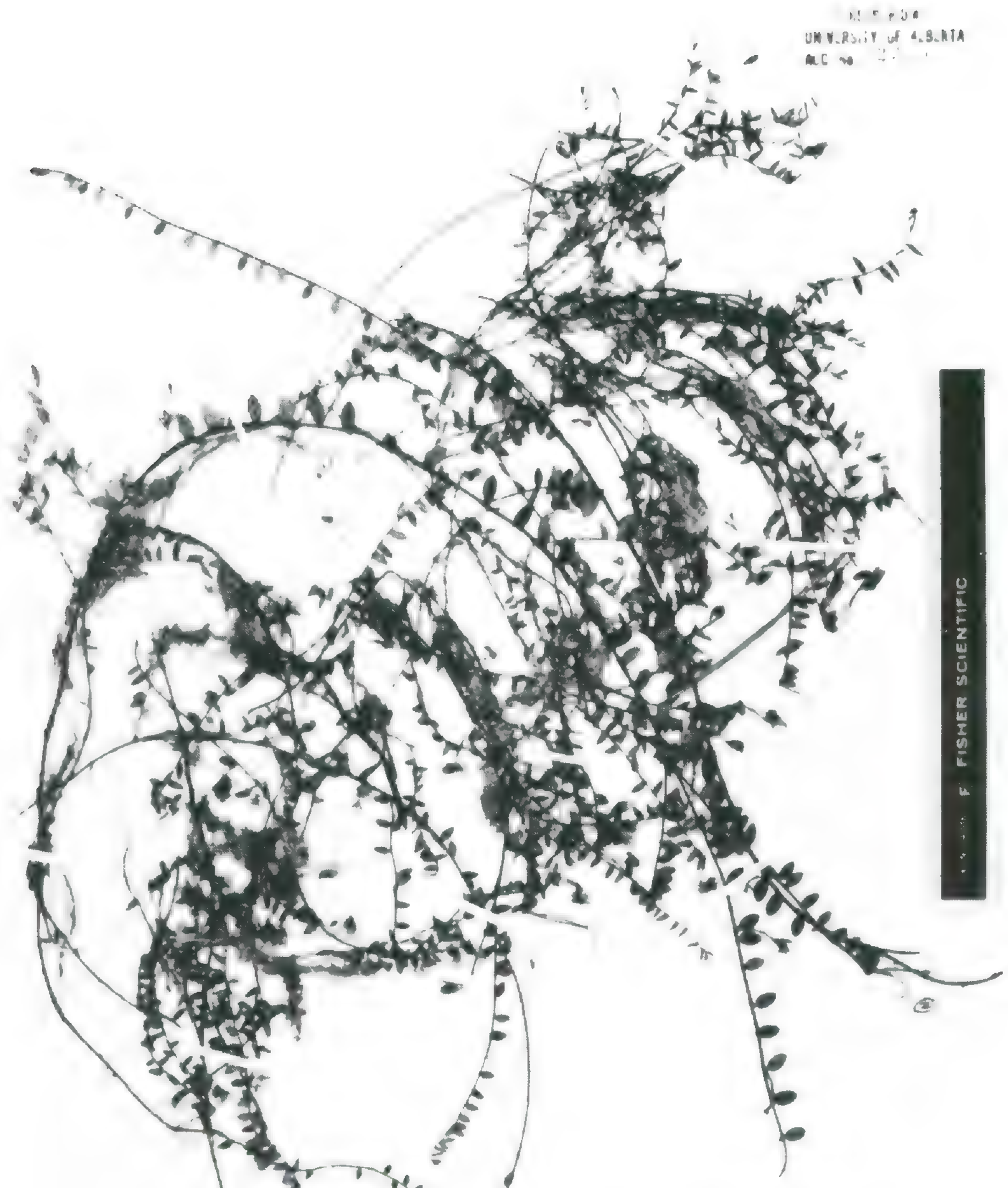


Figure 12. Herbarium collection containing more than one vine of *V. oxycoccus*.

transplanted vines with revolute leaves from exposed hummocks to the shady side of black-spruce clumps and to terraria in the greenhouse and in both places the next set of innovations had flat leaves. Moreover, seedlings, greenhouse grown from open pollinated berries gathered from *V. oxycoccus* plants with strongly revolute leaves, produced quite flat leaves during the winter which became progressively more inrolled as the seasons progressed.

Chromosome counts revealed no surprises: collections of *Vaccinium macrocarpon* pollen mother cells from Nova Scotia and Ontario were consistently diploid (n = 12) and all pollen mother cells of *V. oxycoccus* from Nova Scotia, Quebec and Ontario were consistently tetraploid (n = 24). Provenance of plants from which counts were made are marked with an asterisk in the appendix of collecting sites. Vouchers are at ACAD.

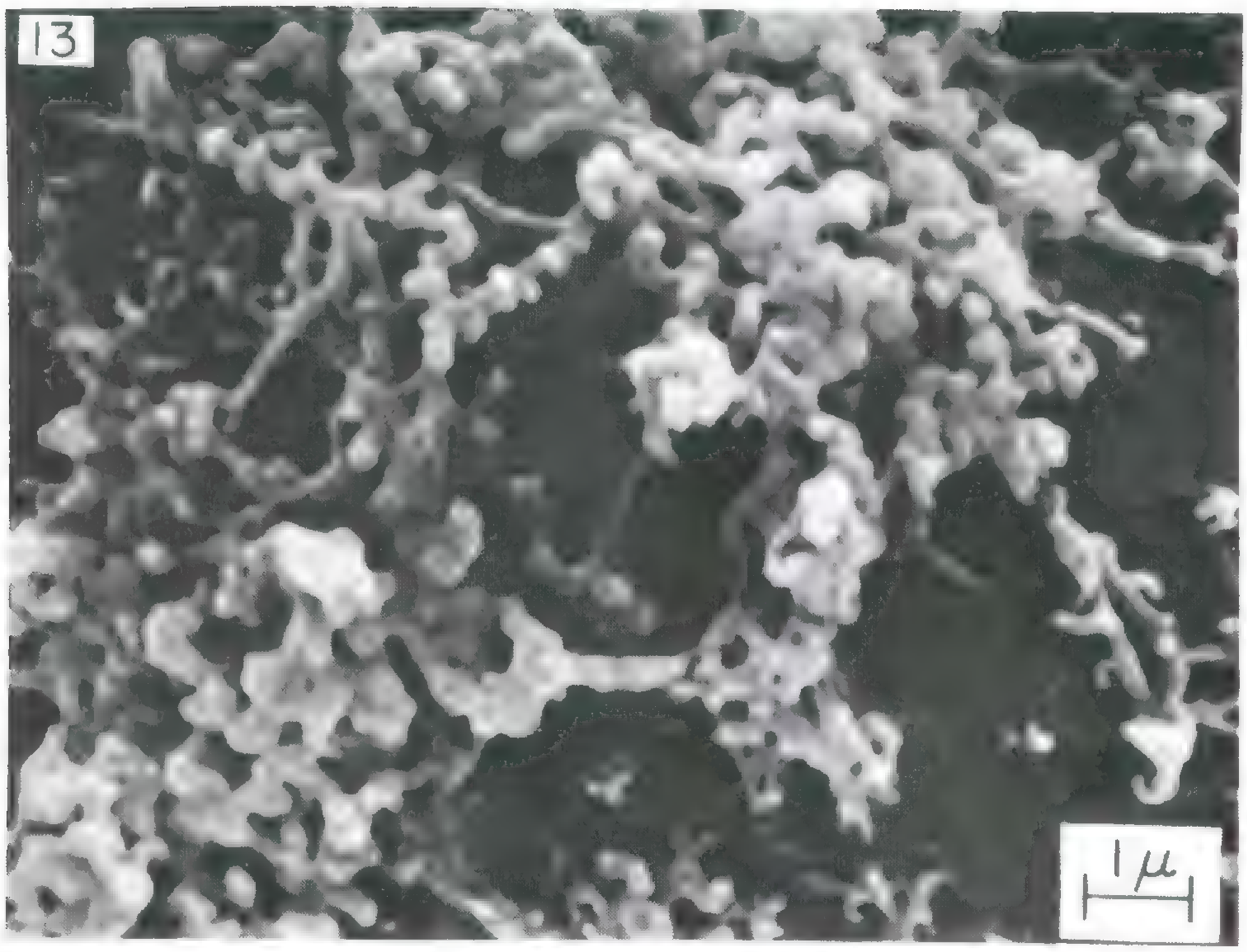
In fine, these analyses suggest that *Vaccinium* § *Oxycoccus* consists of two rather heterogeneous groups, discriminated primarily on the basis of size (figure 11 and table 2), one of which fits into *V. macrocarpon* Aiton and the other into *V. oxycoccus* L. That these clusters ought to be recognized at the species level is further enhanced by the lack of crossing success between the groups. In the areas of sympatry, the groups are temporally separated by two to three weeks at anthesis as well; for example, in Nova Scotia *V. oxycoccus* blooms on the 27th of June ± 13 days and *V. macrocarpon* on the 19th of July ± 9 days. Similar differences in the time of anthesis were observed by Bell & Burchill (1955), who also found that in the resting stage, *V. oxycoccus* bract, sepal, and stamen primordia are differentiated only, there is no sign of stamen and carpel primordia; whilst in *V. macrocarpon* the stamen and carpel primordia show some signs of differentiation.

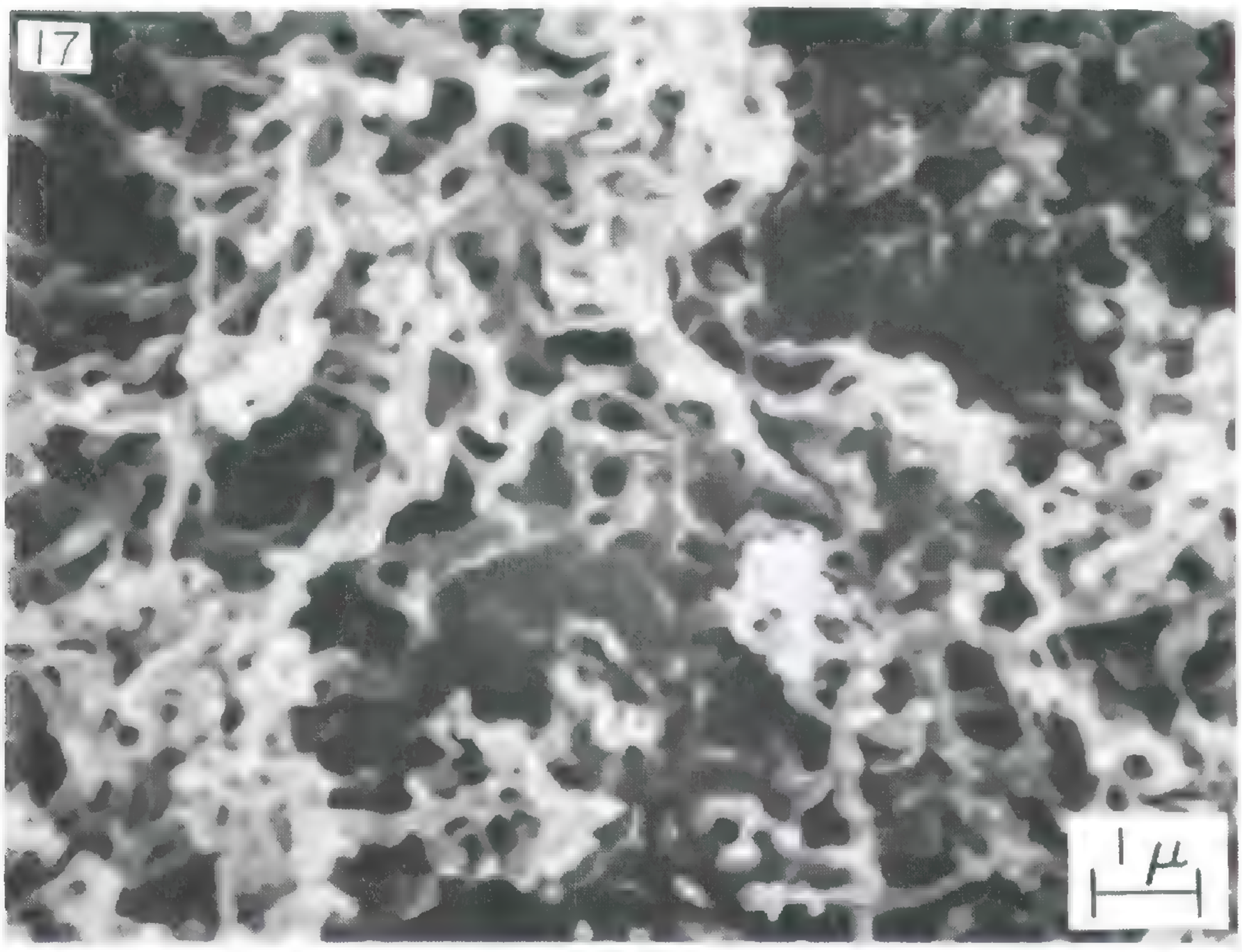
TAXONOMY

Vaccinium § Oxycoccus (Hill) Koch, Fl. Germ. and Helv. 474. 1837.

Oxycoccus [Tourn] Hill, Brit. Herb. 324. 1756.
Oxycoccus [Tourn] Adams. Fam. ii. 164. 1763.
Oxycoccus [Tourn] Persoon, Syn. Plant. **1.** 419. 1805.
Vaccinium § *Oxycoccus* [Tourn] A. Gray, Manual 1st ed. p. 260. 1848.

Trailing vines; branches woody, slender, flexible, terete, glabrous or pubescent; leaves alternate, persistent, almost sessile, margin





Figures 13, 17. Glaucescence of the abaxial leaf surface. 13. Wax rodlets, *Vaccinium macrocarpon*. **17.** Wax rodlets, *V. oxycoccus*.

entire; flowers 4-merous, solitary or in small clusters, axillary or apparently terminal, nodding on long slender pedicels; corolla white to dark pink, lobes nearly cleft to the base, strongly recurved at anthesis; anthers 8, awnless but with long slender tubules; ovary 4-celled, fruit a red, several seeded, berry.

KEY TO THE SPECIES

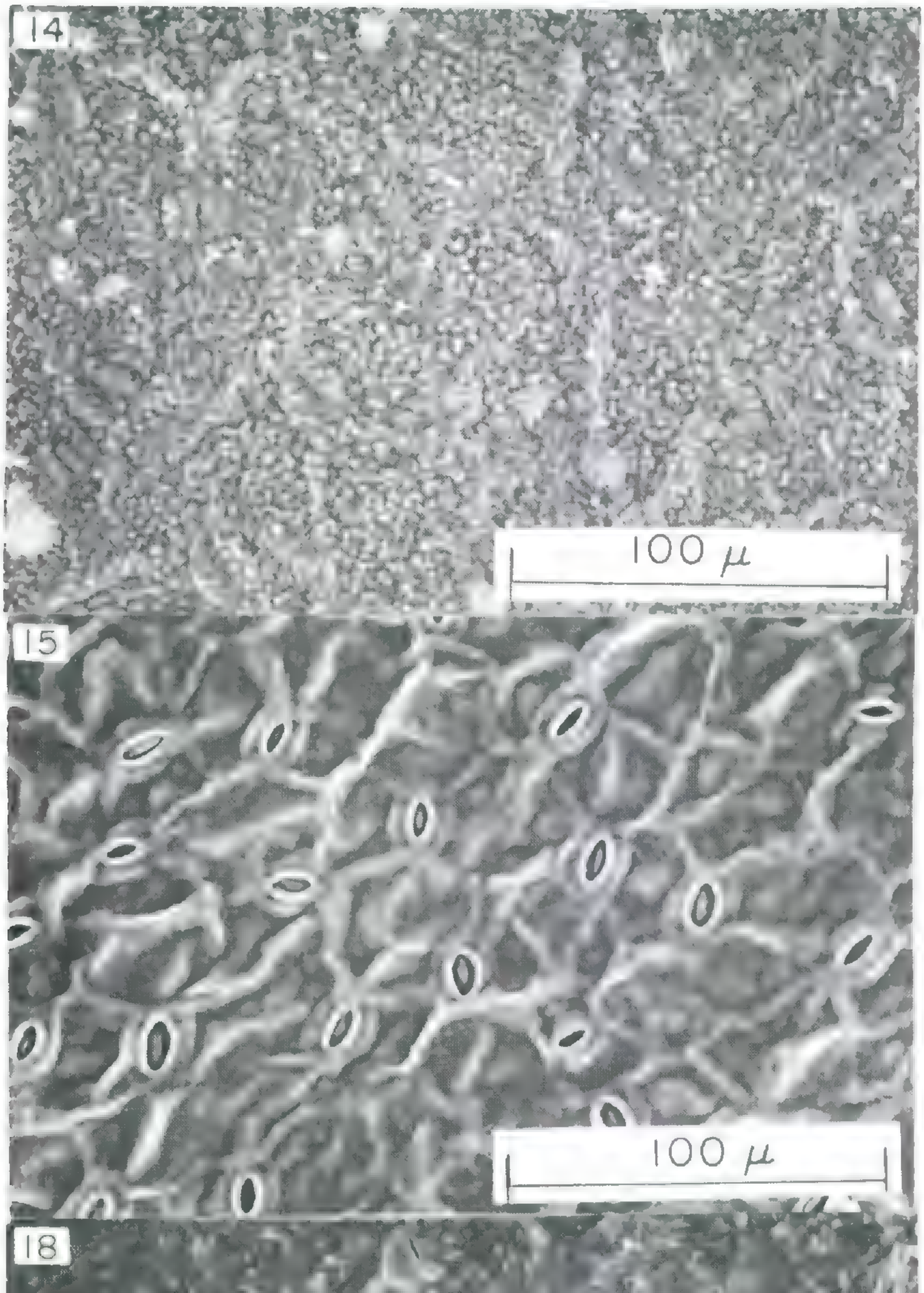
A. Leaves narrowly elliptic, largest usually > 1 cm long; pedicels with leaf-like bracts > 1 mm wide ..... 1. *V. macrocarpon*
AA. Leaves ovate, largest usually < 1 cm long, margin often inrolled; pedicels with red scale-like bracts, < 1 mm wide, sometimes absent ..... 2. *V. oxycoccus*

1. **Vaccinium macrocarpon** Aiton, Hort. Kew. ed. i.ii.**13.** 1789.

V. oxycoccus var. *oblongifolium* Michx. Fl. Bor. Am. **1:** 228. 1803.
V. oblongifolium (Michx) Hort. ex Dun in D.C. Prod. **vii.** 576. 1824.
V. propinquum Salisb. Prod. 291. 1796.
V. macrocarpon f. *eburna* MacKeever, Rhodora **64:** 351. 1962.
Oxycoccus macrocarpus (Aiton) Pers. Syn. Plant. **1.** 419. 1805.

Trailing woody vine; innovations from axillary buds, frequently erect or ascending, 4–15 cm high. Twigs of the current season terete, golden brown, glabrous, rarely pubescent. Leaves narrowly elliptic, elliptic, rarely oblong; (2)3–4(5) mm wide, (5)7–10(18) mm long; green above, glaucous below with the wax so thick that it frequently obscures the stomata (figures 13, 14, 15); margin entire, scarcely revolute. Flowers borne singly in the axils of reduced leaves at the base of current shoots. Pedicels slender, 2–3 cm long, glabrous or pubescent, bearing a pair of green bracts 1–2 mm wide. Calyx lobes 4, very small. Corolla lobes 4, white to pink, strongly reflexed at anthesis. Stamens 8, filaments usually stiffly pubescent along the margins, rarely entirely pubescent or glabrous; anther sacs awnless, tubules long slender 1–2 mm long; pollen tetrads 32–37 μ in diameter. Style 5–7 mm long, glabrous. Berry red, 9–14 mm in diameter, locules 4, each of which has 2 to 7 large brown seeds (figure 16). Chromosome number $2n = 24$.

RANGE: Newfoundland west to central Minnesota south to northern Illinois, northern Ohio and central Indiana and in the Appalachian


14
100 μ
15
100 μ
18
100 μ

Mountains to Tennessee and North Carolina. Its mass centre lies between 40° and 50°N and 70° and 80°W (figure 17). The only report of *V. macrocarpon* occurring north of 50° latitude comes from Sir Joseph Banks (see Lysaght 1971: 69 and 341 where it is argued that the Banksian specimen came from the Bay of Isles (near Cornerbrook) via Wilkinson from James Cook in 1767 rather than from "The Illettes" near Hare Bay in the vicinity of St. Anthony). Aside from the dubious Banksian record, there are in the various herbaria consulted no other specimens extant to support this claim, nor after a diligent 2-day search of the headlands near St. Anthony did I find the plant.

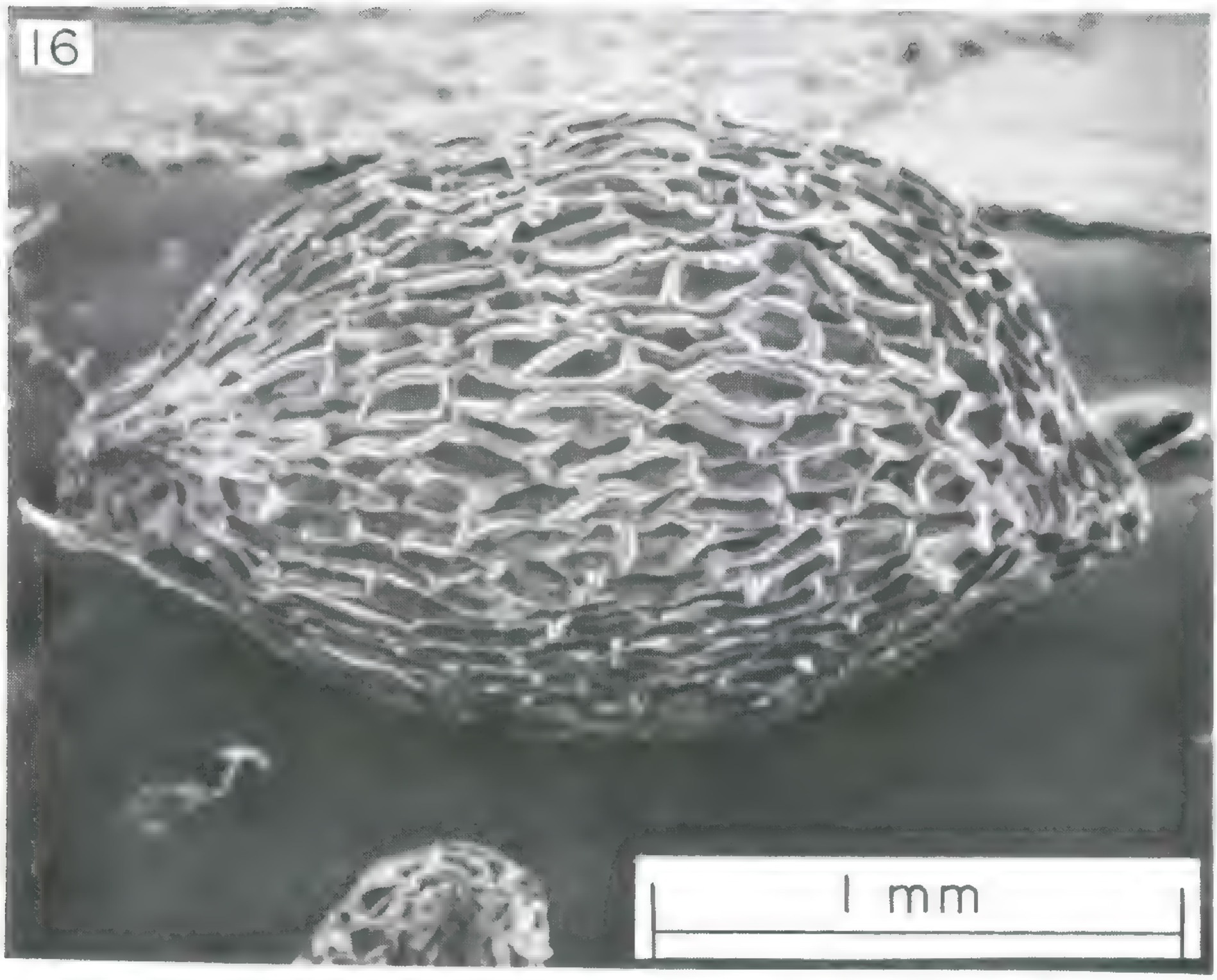
Currently the species is quite rare if not extirpated in Illinois, Ohio, Maryland, North Carolina and Tennessee.

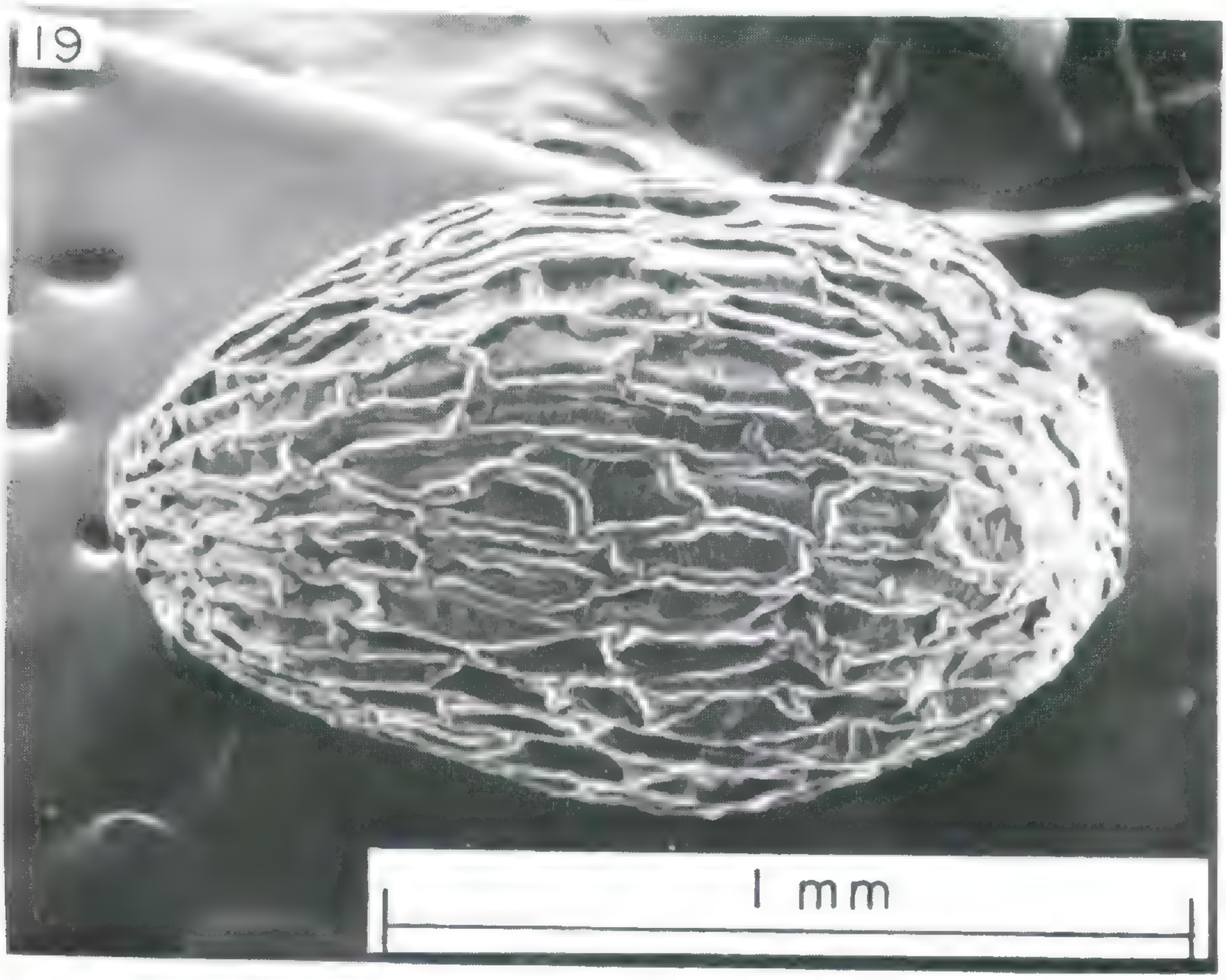
Introduced and adventive along the eastern shore of Maryland (Brown & Brown, 1972) as well as on Lulu Island near Vancouver, British Columbia and several localities in Washington and Oregon. In Europe also the species has been introduced and has become feral in Britain, Germany, Switzerland, and the Netherlands (Popava in Tutin et al. 1972).

TYPE LOCALITY: "Native of North America". Introduced at Kew in 1760 by Mr. James Gordon. Type at BM, seen in 1975. According to Lysaght (1971:341) Aiton's description was based on material from James Gordon as well as on Ehret's plate and not on Banksian material.

HABITAT: open bogs, swamps, mires, wet shores, headlands, and occasionally on poorly drained upland meadows. Occurrence is restricted to acid soils and peat. The pH for 27 soils and peaty substrates tested ranged from a low of 4.8 in bogs to a high of 6.1 in old fields. In open bogs, *V. macrocarpon* is frequently associated with the *Carex-Chamaedaphne calyculata* community at the edge of the floating mat. The species of *Carex* associated with *V. macrocarpon* varies, however: for example, *Carex canescens* (Pers.) Poir in southern New Hampshire (Barrett 1964); *Carex rostrata* Stokes in the Cranberry Glades of West Virginia (Darlington, 1943); *Carex lasiocarpa* Ehrh. in northern Michigan (Gates, 1942); *Carex nigra* (L.) Reichard in Nova Scotia (Hicks, et al., 1968).

Figures 14, 15, 18. Glaucescence of abaxial leaf surfaces. 14, 15. *Vaccinium macrocarpon*. **14,** Glaucescence thick enough to obscure stomata; **15,** Removal of glaucescence reveals stomata. **18.** *V. oxycoccus:* glaucescence thick enough to obscure several stomata.


16
1 mm


19
1 mm

PHENOLOGY: south of 45° N flowering occurs between mid June and mid July and north of 45° N between mid July and mid August. Reproduction is amphimictic, the flowers perfect, protandrous, and entomophilous. Roberts (1978) has found that solitary bees are most efficient at removing pollen from *Vaccinium macrocarpon* flowers, followed by *Bombus* spp. with *Apis mellifera* as the least efficient pollinator; the latter is also inefficient at removing nectar. According to Moeller (1978) in unfertilized flowers the petals turn rosy and persist for several weeks but prompt fertilization causes the petals to drop in a few days.

After pollination, 80-85 days are required for seed set; seed production is a function of pollinator activity. Moeller (1978) found that the plant from which bees were excluded had 6 seeds berry compared to 12–14 seeds berry where bees had been permitted to forage. Hall & Aalders (1965) found that berry weight is a function of seed number with each additional seed contributing some 36 mg to total berry weight.

Although the berries turn a deep red in the autumn, and the large seeds are plump and brown, germination studies by Devlin, et al. (1974, 1976) and Devlin and Karczmarczyk (1975, 1977) among others have shown indubitably that seeds harvested in the autumn require heat, high light intensities, ultraviolet, gibberellic acid, or scarification to induce germination. Under natural conditions, the berries hold through winter, and seeds taken from these berries germinate promptly and en masse without pretreatment unless they have been exposed to frequent inundations of salt water during the winter (tables 3 and 4).

2. **Vaccinium oxycoccus** Linnaeus, Sp. Pl. 351. 1753.

V. palustre Salisb. Prod. 291. 1796.

V. microcarpum (Turcz.) Hook. f. Trans. Linn. Soc. **xxiii**:334. 1861.

V. microcarpum (Turcz. ex Rupr.) Schmalt. Trudy-Imp.S. Peterb. Obšč. Estestv. **2:** 149. 1871.

V. hagerupii (L. & L.) Ahokas, Ann. Bot. Fenn. **8:** 255. 1971.

V. oxycoccus var. *ovalifolium* Michx. Fl. Bor. Am. **1:** 228. 1803.

V. oxycoccus var. *intermedium* Gray. Syn. Fl. N. Am. ed 2.2 pt. 1: 396. 1886.

V. oxycoccus var. *microcarpum* (Turcz.)

V. oxycoccus var. *microphylla* (Lange) Rousseau & Raymond, Nat. Can. **79:** 82. 1952.

Figures 16, 19. Seeds and seed coats. **16.** *Vaccinium macrocarpon.* **19.** *V. oxycoccus*

V. oxycoccus f. *parvifolia* Kurtz. Engl. Bot. Jahrb. **19:** 393. 1894.
V. oxycoccus f. *obovatum* Lepage, Nat. Can. **81:** 259. 1954.
V. macrocarpon f. *dahlei* Finlay & Core, Castanea **38:** 408. 1973.
Oxycoccus quadripetala Gilib. Fl. Lituan **i:**5. 1781.
O. europaeus Pers. Syn. Plant. **1:** 419. 1805.
O. palustris Pers. Syn. Plant **1:** 419. 1805.
O. vulgaris Pursh, Fl. Am. Sept. 1814.
O. microcarpus Turcz. ex Rupr. in Beitr. Pfl. Russ. Reich **4:** 56. 1845.
O. oxycoccus (L.) MacM. Bull. Torr. Bot. Club **19:** 15. 1892.
O. intermedium (A. Gray) Rydb. Fl. Rocky Mts. 646. 1065. 1917.
O. ovalifolius (Michx.) Porsild, Can. Field-Nat. **54:** 116. 1938.
O. hagerupii Löve & Löve, Bot. Not. **114:** 40. 1960.
O. oxycoccus intermedius (A. Gray) Piper, Contrib. U.S. Nat. Herb. **11:** 444. 1906.
O. palustris ssp. *microphylla* (Lange) Löve & Löve, Univ. Colo. Stud. Biol. Ser. no. **17:** 28. 1965.
O. palustris var. *intermedius* (A. Gray) Howell, Fl. N.W. Am. **1:** 413. 1901.
O. oxycoccus var. *intermedius* (A. Gray) Farwell, Papers Mich. Acad. Sci. **2:** 35. 1923.
O. quadripetala var. *microphylla* (Lange) M. P. Porsild, Medd. Grönl. **77:** 42. 1930.
O. palustris var. *ovalifolius* (Michx.) Seymour, Am. Mid. Nat. **40:** 935. 1953.
O. palustris f. *microphylla* Lange, Consp. Fl. Grönl **2:** 267. 1887.

Trailing wiry woody vine; innovations from axillary buds, often ascending 1–3 cm high. Twigs of the current season terete, very slender, dark brown to red, glabrous to pubescent. Leaves ovate, occasionally elliptic, (1)2–3(5) mm wide, (3)5–6(10) mm long; green above, glaucous below with wax so thick that it frequently obscures the stomata (figures 18, 19); margin entire; frequently revolute and often strongly so. Flowers borne singly in the axils of reduced leaves at the base of current shoots (figure 8), however on most vines the leafy portion of the fertile shoot especially north of 50° latitude does not develop giving the illusion that *V. oxycoccus* has an inflorescence consisting of a short rachis bearing 1–4 flowers on long slender pedicels (figures 1, 2). Pedicels slender, 2–3 cm long, glabrous to pubescent, bearing (0)2(5) reddish scaly bracts $<$ 1 mm wide. Calyx lobes 4, very small. Corolla lobes 4, white to deep pink, strongly reflexed at anthesis. Stamens 8, filaments usually stiffly pubescent along the margins, occasionally pubescent, rarely glabrous; anther sacs awnless, tubules slender 1 mm long; pollen tetrads 34–46 μ in diameter. Style 3–4 mm long, glabrous. Berry, at first punctate, later turning deep red, 6–12 mm in diameter, locules 4,

Figure 20. Distribution of *Vaccinium macrocarpon*.

Table 4. **Germination characteristics of *Vaccinium macrocarpon* Aiton.**

Coll. #	date collected	date sown	# seeds sown	germination (%)	first radicle emerges (days)	first dicotyledon (days)	first true leaf (days)
NS 1 .	27979*	9.XII.80	25	4	30	53	55
NS 4 .	27979	"	40	0	--	--	--
NS 5 .	27980	"	48	0	--	--	--
NS 1 .	71079	"	107	0	--	--	--
NS 2 .	71079	"	87	0	--	--	--
NS 3 .	71079	"	90	0	--	--	--
NS 1 .	81079	"	141	0	--	--	--
NS 1 .	111080	"	142	2	31	41	54
NS 1 .	131080	"	131	0	--	--	--
NS 2 .	131080	"	124	3	36	44	60
NS 3 .	131080	"	131	0	--	--	--
Ont. 2 .	281080	"	79	82	14	25	31
Ont. 1 .	311080	"	49	100	17	27	33
NS 1 .	1481	1.IV.81	52	96	8	17	23
NS 1 .	1481	"	34	76	9	20	25
NS 1 .	1481	"	23	100	9	19	25
NS 2 .	1481	"	60	100	8	17	23

NS 1 . 17481	21.IV.81	263	99	9	20	25
NS 2 . 17481	"	230	93	7	20	25
NS 4 . 18481	"	74	94	8	17	24
NS 5 . 18481**	"	414	22	9	17	24
NS 6 . 18481**	"	203	9	7	20	24
NS 7 . 18481**	"	225	1	7	20	24
NS 8 . 18481**	"	207	6	9	21	30
NS 2 . 27481	28.IV.81	6	100	10	21	26
NS 3 . 27481	"	39	100	10	20	25
NS 1 . 201080***	"	167	44	18	30	36
Ont. 1 . 311080***	"	19	78	15	24	30
Ont. 3 . 6581	15.V.81	59	40	11	19	24
Ont. 4 . 6581	"	24	95	11	21	23

NOTE — *seeds stored in a sealed mason jar at 1° C until sown.
**berries submerged in brackish pools along headlands.
***seeds kept in berries and frozen at −20° C until sown.

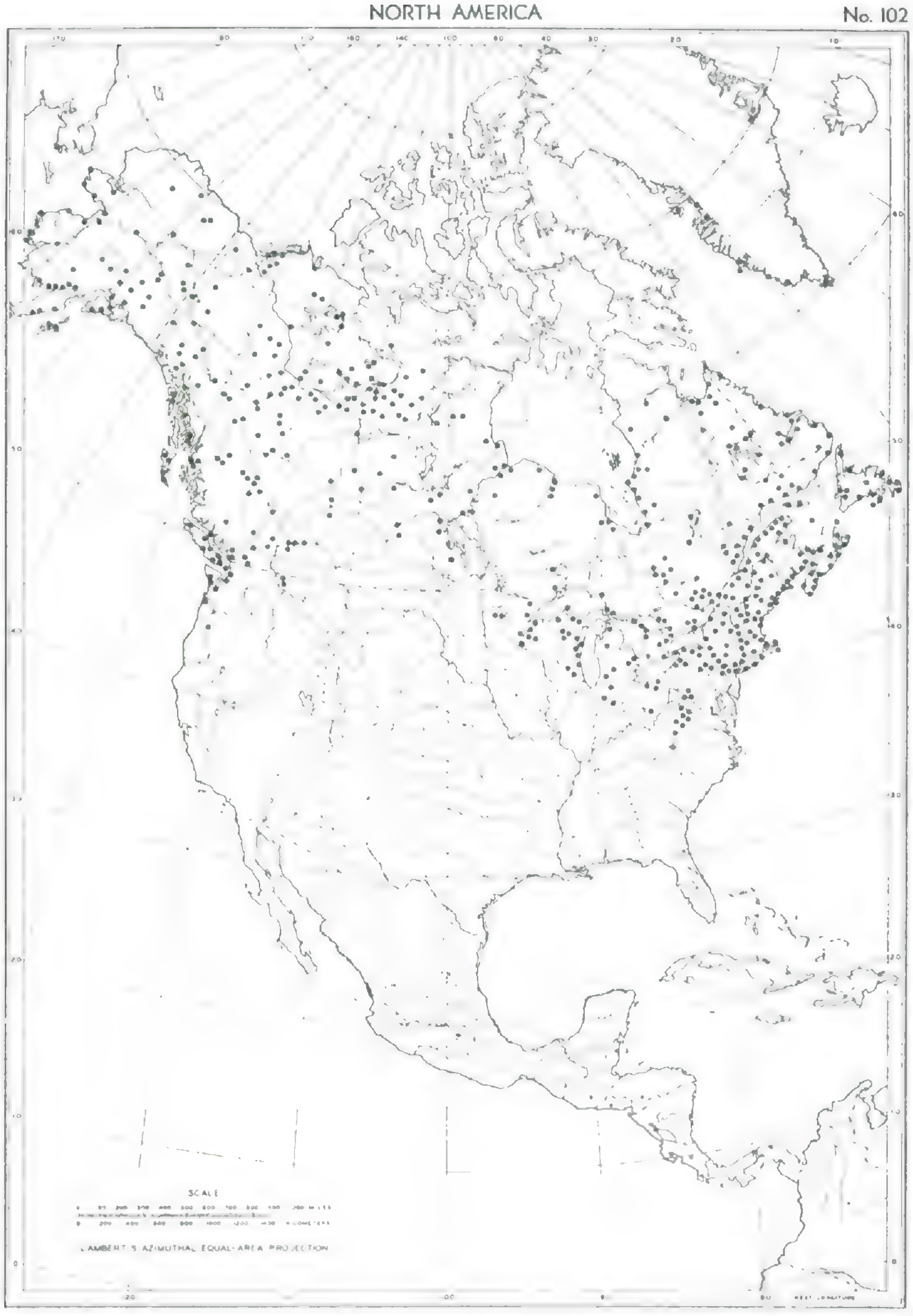


Figure 21. Distribution of *Vaccinium oxycoccus*.

each of which has 1–4 large brown seeds (figure 20). Chromosome number: 2n = 24, 48, 72.

RANGE: Circumboreal, in North America the species is absent from the Arctic Archipelago including Baffin Island, and extends southwards to Central Oregon in the Cascades and to Virginia in the Appalachians (figure 21).

TYPE LOCALITY: Sweden, Type at LINN, *#497.18,* seen in 1975.

HABITAT: half buried in *Sphagnum* hummocks of bogs, the muskegs of the taiga and the low arctic tundra. This habitat is best described as oligotrophic with low pH (2.9–3.8), few exchangeable cations (Grandtner, 1960) and little available nitrogen and phosphorus (Small, 1972).

PHENOLOGY: Anthesis occurs from mid-May to mid-June in New Jersey, eastern New York, Connecticut, Massachusetts, southeastern Ontario, Washington and southern British Columbia; from mid-June to mid-July in the Appalachians, Pennsylvania, New Hampshire, Maine, Vermont, northern New York, central Ontario, adjacent Quebec and the Maritimes as well as the West in that area west of 100° longitude and south of 65° N. In the remainder of the continent the species flowers from mid-July to mid-August. Reproduction is amphimictic, the flowers perfect, protandrous and entomophilous. *Bombus* spp. and solitary bees are the most frequent pollinators. After pollination, 85–90 days are required for seed set in New England, the Maritimes and southern Ontario and Quebec, but only 35–45 days in the low arctic regions. Seed set and seed weight are invariably less than in *V. macrocarpon* even where the two species share the same bog (table 2).

As in *Vaccinium macrocarpon, V. oxycoccus* berries hold over winter and are dispersed by water, birds, and mammals in early spring. As in *V. macrocarpon,* seeds collected in the spring germinate most readily (table 5), except that the rate of germination is significantly higher in *V. oxycoccus* in both the vernal and autumnal trials. Moreover berries collected in late October and early November contain seeds ready to germinate so whatever the after ripening requirement may be, it has been met before the actual onset of winter in *V. oxycoccus* but not in *V. macrocarpon,* which is to be expected since it flowers 3 weeks later therefore also sets seeds 3 weeks later than *V. oxycoccus.*

Table 5. **Germination characteristics of *Vaccinium oxycoccus* L.**

Coll. #	date collected	date sown	# seeds sown	germination (%)	first radicle emerges (days)	first dicotyledon (days)	first true leaf (days)
NS 1	. 16979*	9.XII.80	36	0	--	--	--
NS 2	. 16979	"	65	0	--	--	--
NS 3	. 16979	"	53	3	19	33	50
NS 2	. 27980	"	59	5	17	33	59
NS 3	. 27980	"	50	0	--	--	--
NS 2	. 81079	"	33	0	--	--	--
NS 3	. 81079	"	57	0	--	--	--
NS 2	. 91079	"	63	3	19	29	36
NS 6	. 131080	"	75	2	21	32	39
NS 7	. 131080	"	68	4	27	33	44
NS 1	. 141080	"	19	5	21	33	39
P.Q. 1	. 261080	"	39	79	14	25	29
Ont. 1	. 281080	"	26	26	17	30	36
P.Q. 1	. 21180	"	174	96	14	25	29

NS 1 . 18481	21.IV.81	62	96	9	20	25
NS 2 . 18481	"	55	100	9	20	29
NS 3 . 18481	"	267	89	9	20	29
NS 1 . 27481	"	24	100	12	21	30
P.Q. 1 . 261080**	"	52	98	16	22	27
P.Q. 1 . 4581	15.V.81	63	99	11	19	23
P.Q. 2 . 4581	"	185	96	10	19	23
Ont. 1 . 6581	"	214	83	11	19	23
Ont. 1 . 6581	"	65	84	11	19	24
P.Q. 1 . 12581	"	16	87	11	19	24
P.Q. 2 . 12581	"	106	100	7	16	22

NOTE — *seeds stored in a sealed mason jar at 1° C until sown.
**seeds kept in berries and frozen at −20° C until sown.

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REFERENCES

Barrett, P. E. 1966. The relationship of some physical and edaphic factors to plant succession in a southern New Hampshire peat bog. M.Sc. Thesis, University of New Hampshire.

Bell, H. P., & J. Burchill. 1955. Flower development in the lowbush blueberry. Can. J. Bot. **33:** 251–258.

Boivin, B. 1967. Flora of the Prairie Provinces. Phytologia **15:** 121–159, 329–446; **16:** 1–47.

Brown, R. G., & M. L. Brown. 1972. Woody plants of Maryland. Distributed by Student Supply Store, University of Maryland, College Park.

Camp, W. H. 1944. A preliminary consideration of the biosystematy of *Oxycoccus*. Bull. Torrey Bot. Club **71:** 426–437.

Darlington, H. C. 1943. Vegetation and substrate of Cranberry Glades, West Virginia. Bot. Gazette **104:** 371–393.

Darrow, G. M., W. H. Camp, H. E. Fischer, & H. Dermen. 1944. Chromosome numbers in *Vaccinium* and related groups. Bull. Torrey Bot. Club **71:** 498–506.

Devlin, R. M., & S. J. Karczmarczyk. 1974. The effect of light on cranberry seed germination. Cranberries **38:** 3 & 16.

_____. 1975. Effect of light and gibberellic acid on the germination of 'Early Black' cranberry seeds. Hort. Res. **15:** 19–22.

_____. 1977. Influence of light and growth regulators on cranberry seed dormancy. J. Hort. Sci. **52:** 283–288.

Devlin, R. M., S. J. Karczmarczyk, & K. H. Deubert. 1976. The influence of abscisic acid in cranberry seed dormancy. Hort. Science **11:** 412–413.

Fernald, M. L. 1902. The variations and distribution of American cranberries. Rhodora **4:** 231–237.

_____. 1950. Gray's manual of botany. 8th ed. American Book Co., New York.

Gates, F. C. 1942. The bogs of northern lower Michigan. Ecol. Monogr. **12:** 215–254.

Gleason, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. New York Botanical Garden, New York.

Grandtner, M. M. 1960. La forêt de Beauséjour, comté de Lévis, Québec. Fonds rech. forest, Univ. Laval, Contr. No. 7, 62 p.

Hagerup, O. 1928. Morphological and cytological studies of *Bicornes*. Dansk. Bot. Arkiv **6:** 1–26.

_____. 1940. Studies on the significance of polyploidy. IV. *Oxycoccus*. Hereditas **26:** 399–410.

HALL, I. V., & L. E. AALDERS. 1965. The relation between seed number and berry weight in the cranberry. Can. J. Plant Sci. **45:** 292.

HALL, S. H., & G. J. GALLETTA. 1971. Comparative chromosome morphology of diploid *Vaccinium* species. J. Am. Soc. Hort. Sci. **96:** 289–292.

HARA, H. 1956. Contributions to the study of variations in the Japanese plants closely related to those of Europe or North America. Pt. 2. Jour. Fac. Sci. Tokyo Imp. Univ., Sect. 3, Bot. **6:** 343–391.

HICKS, J. L., I. V. HALL, & F. R. FORSYTH. 1968. Growth of cranberry plants in pure stands and in weedy areas under Nova Scotian conditions. Hort. Res. **8:** 104–112.

JÖRGENSEN, C. A., T. H. SORENSEN, & M. WESTERGARD. 1958. The flowering plants of Greenland: a taxonomical and cytological survey. K. Danske Videnskab. Selskab. Biol. Skrift. **9:** 1–172.

LÖVE, A. & D. LÖVE. 1956. Cytotaxonomical conspectus of the Icelandic Flora. Acta Horti Gothoburgensis **20:** 65–291.

LYSAGHT, A. M. 1971. Joseph Banks in Newfoundland and Labrador, 1766. Faber & Faber, London.

MOELLER, F. E. 1979. How long must honey bees be present to effectively set a crop of cranberries? Proc. IVth Int. Symp. on Pollination, Oct. 11-13, 1978. Md. Agric. Exp. Sta. Spec. Misc. Publ. **1:** 171–173.

NEWCOMER, E. H. 1941. Chromosome numbers of some species and varieties of *Vaccinium* and related genera. Proc. Am. Soc. Hort. Sci. **38:** 468–470.

POJAR, J. 1974. The relation of the reproductive biology of plants to the structure and function of four plant communities. Ph.D. Thesis, University of British Columbia, Vancouver.

POLUNIN, N. 1959. Circumpolar Arctic flora. Clarendon Pr., Oxford, Eng. 514 p.

PORSILD, A. E. 1938. The cranberry in Canada. Can. Field-Nat. **52:** 116–117.

_____, & W. J. CODY. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, Ottawa. 667 p.

ROBERTS, R. B. 1979. Energetics of cranberry pollination. Proc. IVth Int. Symp. on Pollination Oct. 11-13, 1978. Md. Agric. Exp. Sta. Spec. Misc. Publ. **1:** 431–440.

RODRIGUES, L. A. 1963. A systematic study of variation in the small-fruited cranberry. M.Sc. Thesis, University of New Hampshire.

ROHWEDER, H. 1937. Versuch zur Erfassung der mengemassigen Bedeckung des Darss und Zingst mit polyploïden Pflanzen: ein Beitrag zur Bedeutung der Polyploidie bei der Eroberung neuer Lebensräume. Planta **27:** 501–549.

SCOGGAN, H. J. 1979. The flora of Canada. pt. 4. *Dicotyledoneae (Loasaceae* to *Compositae).* National Museum of Natural Sciences. Publ. in Bot. 7(4).

SHISHKIN, B. K. & E. G. BOBROV. 1967. Flora of the U.S.S.R. XVIII. *Metachlamydeae. In:* Academy of Science of the U.S.S.R. Botanical Institute im V. L. Komarov. Flora of the U.S.S.R. Transl. from Russian. Israel Program for Scientific Translations, Jerusalem.

SLEUMER, H. 1941. Vacciniodeen Studien. Bot. Jahrb. Sonder.-Abdr. **71:** 375–510.

SMALL, E. 1972. Ecological significance of four critical elements in plants of raised bogs. Ecology **53:** 498–503.

SNEATH, P. H. A., & R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman, San Francisco, CA.

STEVENS, P. F. 1969. Taxonomic studies in the *Ericaceae*. Ph.D. Thesis, University of Edinburgh.

TISCHLER, G. 1934. Die Bedeutungen der Polyploidie fur die Verbreitung der Angiospermen, erlautert an den Arten Schleswig Holsteins, mit Ausblicken auf andere Florengebiete. Bot. Jahrb. **67**: 1–36.

TUTIN, T. G., V. H. HEYWOOD, ET AL. 1972. Flora Europaea. V. **3**. *Diapensiaceae* to *Myoporaceae*. Cambridge University Press, London.

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APPENDIX 1. LOCATION OF SAMPLING SITES

*Chromosome number determined for one or more plants.

1. Jct. of Webbs Mill Brook and SR539, Ocean County, New Jersey; mire; *V. macrocarpon*.
2* Mast Way, Lee, Strafford County, New Hampshire; bog; *V. oxycoccus* (n = 24) 2 plants.
3. Quoddy Head, Washington County, Maine; hummocks on high moor; *V. oxycoccus*.
4. Drakes Island, Rachel Carson Wildlife Refuge, York County, Maine; red maple swamp; *V. macrocarpon*.
5* Mud Lake, 1 km west of Black River Lake, Kings County, Nova Scotia; bog; *V. oxycoccus* and *V. macrocarpon* (n = 12) 6 plants.
6* 4 km E of Kingston along Hwy. 1, Kings County, Nova Scotia; boggy depressions; *V. macrocarpon* (n = 12) 1 plant.
7. Little Lorraine, Wild Cove, Cape Breton County, Nova Scotia; rocky headlands; *V. macrocarpon*.
8. Leap Frog Lake, Port Maitland, Yarmouth County, Nova Scotia; boggy margin; *V. oxycoccus*.
9. 8 km west of Birchtown along Hwy. 3, Shelburne County, Nova Scotia; raised bog and boggy barrens; *V. oxycoccus*.
10. 5 km N of exit 46 along Hwy. 104, Richmond County, Cape Breton Island, Nova Scotia; raised bog; *V. oxycoccus*.
11. 1.5 km N of West Dover along Hwy. 333, Halifax County, Nova Scotia; boggy barrens; *V. oxycoccus*.
12. French Mountain, Cape Breton Highlands, Inverness County, Nova Scotia; extensive high moor; *V. oxycoccus*.
13. Red Head, Port Maitland, Yarmouth County, Nova Scotia; mire; *V. oxycoccus*; headlands, *V. macrocarpon*.
14* 4 km west of West Branch, Pictou County, Nova Scotia; abandoned, poorly drained *Festuca ovina* meadow; *V. macrocarpon* (n = 12) 1 plant.
15* Portuguese Cove Headlands, Halifax County, Nova Scotia; headlands; *V. macrocarpon* (n = 12) 2 plants; boggy depressions, *V. oxycoccus* (n = 24) 1 plant.

16* Kennington Cove, Cape Breton County, Nova Scotia; raised bog, *V. oxycoccus* (n = 24) 2 plants; headlands, *V. macrocarpon* (n = 12) 5 plants.

17 2 km SW of Bonavista, Massive headlands, Newfoundland; boggy depression between headlands; *V. oxycoccus*.

18. RT185 at P.Q. - N.B. border, Temiscouata County, Quebec; spruce woods and extensive bogs; *V. oxycoccus* (n = 24).

19* Villeroy, Route 20, Sortie 158, Lotbiniere County, Quebec; raised bog; *V. oxycoccus* (n = 24) 3 plants, *V. macrocarpon*.

20. Along SR8 at Graphite, Warren County, New York; lake margin; *V. macrocarpon*.

21. Westport Bog, 4 km NE of Westport, Leeds County, Ontario; bog; *V. oxycoccus, V. macrocarpon*.

22* Byron Bog, suburban London, Middlesex County, Ontario; bog; *V. oxycoccus* (n = 24) 3 plants; *V. macrocarpon* (n = 12) 1 plant.

23. 1 km W of Heart Lake, near Snelgrove, Peel County, Ontario; bog; *V. macrocarpon*.

24. Mer Bleue, beyond Borthwick Road, Carleton County, Ontario; raised bog; *V. oxycoccus, V. macrocarpon*.

25* Hebert Bog, Upper Rock Lake, Frontenac County, Ontario; bog; *V. oxycoccus* (n = 24) 6 plants; *V. macrocarpon* (n = 12) 4 plants.

26 Fraser River Delta at Richmond Rd #5 and the CNR right-of-way, Lulu Island, British Columbia; disturbed raised bog; *V. macrocarpon*.

APPENDIX II

Citation of Specimens

GREENLAND. Ameralik Fj. Ameragdla Arm. Equaluit, 64°09′N, 50°22′W, *A. E. Porsild 8406* in 1941 (CAN); OTU 2. Amitsuarssuk, 60°08′N, 44°45′W, *Carlo Hansen, Lars Kliim-Nielson, and Benjamin Ølgaard 67–408* in 1967 (CAN); OTU 3. Frederikshaab, 62°, *J. Eugenius* in 1928 (CAN); OTU 47. Godthaab Fj. S. point of Sadlen Island, *A. E. Porsild 12000* in 1942 (CAN); OTU 42. Godthaab Fj., Qornoq Island, 64°30′N, 51°05′W, *A. E. Porsild 8698* in 1942 (CAN); OTU 41.

CANADA.

Alberta. Anzac, S.E. tip of Gregoire Lake, S.E. of McMurray, *M. G. Dumais and K. Anderson 2692* in 1968 (ALTA); OTU 9. 1/2 mi. S. of Ma-Me-O Beach, *G. H. Turner MD. 8332* in 1953 (ALTA); OTU 8. Primrose Lake, 6 mi S of tip of lake, *M. G. Dumais and C. G. Rankin 1287* in 1967 (ALTA); OTU 7.

British Columbia. Cape Beale, Lake Kihha, *S. Hartwell 62503* (UAC). Georgie Lake, Port Hardy, *J. Hett and W. Armstrong 303* in

1964 (UVIC). Lulu Island, Vancouver, *J. W. Eastham 11,434* in 1944 (ALTA). Wolverine Range, near Manson Creek village, N. of Ft. St. James, 55° 40′N, 124° 22′W, *J. A. Calder, D.B.O. Saville and J. M. Fergusson 13690* in 1954 (DAO).

Nova Scotia. Colchester County, Earltown, *A. R. Prince 206* in 1927 (ACAD); OTU 5. St. Paul Island, *J. S. Erskine 53,693* in 1953 (DAO).

N.W.T. Dumpy Lake, near Eldorado Mine, Port Radium, E end of McTavish Arm, Great Bear Lake, 66° 05′N, 118° 02′W, *Hansford T. Shacklette 2766* in 1948 (CAN); OTU 43. Grassy Island, Thelon River, *John S. Tener 259* in 1952 (CAN); OTU 44. Hornby's Bend. Thelon River, *John S. Tener 258* in 1952 (CAN); OTU 45. Keewatin, mouth of Windy River, *F. Harper 2347* in 1947 (CAN); OTU 46. MacKenzie Lowlands, Liard R. Valley, 10 mi. N of B.C. boundary, *W. W. Jeffrey 84* in 1959 (CAN).

Ontario. De Grassi Pt., Lake Simcoe, *E. M. Walker* in 1894 (TRT). Durham County, Newtonville Bog, *J. C. Krug and J. E. Purchase 484* in 1963 (TRT). Grey County, Stewart Lakes, 44° 23′N, 80° 55′W, *G. R. Thaler 182* in 1965 (TRT). Holland Swamp, near Newmarket, *W. C. McCalla* in 1896 (ALTA); OTU 10. London and Parry Sound, *T. J. W. Burgess and D. Burgess* in 1880 and 1881 (TRT). Mador, Snake Lake, *Hastings* in 1907 (TRT). Middlesex, Byron Bog, *W. W. Judd* in 1956 (TRT). N.W. of Nuelton Lake, mouth of Windy Lake, S.W. Keewatin, *Francis Harper 2347* in 1947 (CAN). Wellington County, Brisbane, 3/4 mi. S. just off Hwy. 24, 43° 44′N, 80° 05′W, *G. R. Thaler 119* in 1965 (TRT). Wellington County, Puslinch, *J. J. Stroud* in 1939 (TRT). Wentworth County, 1 mi. S.E of Copetown, *J. H. Soper and J. K. Shields 4735* in 1950 (TRT). York County, Holland R. Marsh, *Roy F. Cain* in 1930 (TRT). York County, Pottageville, *W. R. Watson 2668* in 1926 (TRT).

Yukon. Halfway Lakes, 15 mi. N of Mayo, 63° 48′N, 135° 48′W, *W. A. Calder, J. M. Gillett and D. A. Mitchell 4156* in 1949 (DAO). Jensen Flats, 6 mi. on rd. to Paris fr. Granville, 63° 42′N, 138° 33′W, *J. A. Calder and L. G. Billard 3163* in 1949 (DAO). Peavine Camp, tributary of Porcupine River, 65° 48′N, 138° 35′W, *J. A. Calder and J. M. Gillett 26243* in 1960 (DAO).

UNITED STATES

Alaska. Eagle River, near Juneau, *J. P. Anderson 6351* in 1940 and 1941 (DAO). Lake Spenard, Anchorage, *Dutilly, Le Page and*

O'Neill 20,274 in 1947 (DAO). 2 mi. N of Seward-Kenai-Anchorage rd. junction, Kenai Peninsula, 60° 34′N, 149° 35′W, *J. A. Calder 5757* in 1951 (DAO). Naknek, *W. B. Schofield 1951* in 1952 (DAO). Sterling Hwy. between Kasilof and Homer, Kenai Peninsula, 60° 20′N, 151° 16′W, *J. A. Calder 5417* in 1951 (DAO).

Maine. Aroostook Co., Crystal, *A. R. Hodgdon and William Countryman 19285* in 1971 (NHA). Cumberland Co., Perley Pond, Sebago, *M. L. Fernald, Bayard Long and A. H. Norton 11854* in 1916 (NHA). Washington Co., on hwy. 191 near S.W. corner of Cathance Lake, *Edw. & Susan Johnson 279* in 1970 (NHA). Washington Co., Jonesport, *C. A. Cheever* in 1905 (NHA).

New Hampshire. Carroll Co. Mystery Pond, Ossipee, *A. R. Hodgdon and T. Marsdon Jones 3376* in 1939 (NHA). Carroll Co. Ossipee, Heath Pond Bog, *Irene M. Storks 328* in 1978 (NHA). Carroll Co. Tamworth, *A. R. Hodgdon, Anthony J. Hodgdon, and Alec Lincoln 7819* in 1954 (NHA). Coos Co. Pittsburg, *A. R. Hodgdon and P. Allen, et al. 11941* in 1960 (NHA). Grafton Co. Heath Pond Bog, *Paul Barrett and A. R. Hodgdon 15534* in 1965 (NHA). Hillsborough Co., Greenfield, Hogback Pond, Greenfield State Park, *A. R. Hodgdon, Peter Allen, Henry Baldwin 12724* in 1963 (NHA). Rockingham Co. Kingston Cedar Bog Pond, *A. R. Hodgdon and F. L. Steele 20002* in 1973 (NHA). Rockingham Co. Kingston Jct Rt. 125 and Rt. 111, *Garrett E. Crow 2284* in 1976 (NHA). Strafford Co. Madbury, Barbadack Pond, *Lee Rodrigues and A. R. Hodgdon 12415* in 1962 (NHA). Strafford Co. Barrington, near Winkley Pond, *A. R. Hodgdon and H. A. Giddings 4612* in 1943 (NHA). Strafford Co. Lee, *A. R. Hodgdon and H. Clapp 3383* in 1940 (NHA).

Vermont. Windham Co. Whitingham, "floating Is." anchored ericaceous bog in Lake Sedoga S. of Wilmington, *A. R. Hodgdon 19954* in 1973 (NHA).

FINLAND

South Savo, Sulkava, Partalansaari, Auvila, S. W. shore of Lake Kikolampi, *Marjatta Isoviita* in 1976 (ALTA).

KALMIA ERICOIDES REVISITED.

WALTER S. JUDD

ABSTRACT

Specific limits within the Cuban taxa of *Kalmia* (Ericaceae) are reinvestigated. A single species, *K. ericoides*, with two geographically isolated varieties is recognized. *Kalmia ericoides* var. *ericoides* is limited to Pinar del Río while var. *aggregata* occurs only on the Isle of Pines. The taxa may be readily separated by the indumentum of their young twigs. *Kalmia simulata* is placed in synonymy under var. *aggregata*.

The delimitation of species within the *Kalmia* populations of western Cuba (prov. Pinar del Río) and the Isle of Pines has varied widely (Table 1). Some botanists, e.g., Wood (1961) and Ebinger (1974) have considered all the Cuban Kalmias as members of a single species, *Kalmia ericoides* (with or without recognized varieties), while others, e.g., Roig & Acuña (1957), Alain (1946 & specimen identifications), and Southall and Hardin (1974) have divided the group into three species, i.e., *K. ericoides, K. aggregata,* and *K. simulata,* based upon variation in pubescence (see Figure 1), compactness of the inflorescence, and length of the leaves and/or calyx lobes. Small (1914) recognized only two species, however: at that time *K. simulata* had not been described (see Britton, 1920). Disagreements have also existed as to the geographic distribution of the various recognized taxa (Table 1) and the value of the various characters used in their identification. Therefore the taxonomic relationships between the diverse Cuban populations of *Kalmia* are reassessed here through a detailed study of herbarium materials.

Kalmia ericoides sensu stricto has usually been characterized by the pilose (i.e., with long-celled hairs) and stipitate-glandular pubescence of its leaves and stems. However, the leaves are frequently described as being smooth above (Small, 1914; Roig & Acuña, 1957). Other distinguishing characters are the lax inflorescence (Small, 1914; Roig & Acuña, 1957; Southall & Hardin, 1974; Ebinger, 1974), ciliate calyx lobes (Roig & Acuña, 1957), and pubescent filaments (Small, 1914). *Kalmia aggregata,* described by Small in 1914, is usually distinguished by the densely puberulent and stipitate-glandular pubescence of its leaves and stems, "crowded" leaves (Ebinger, 1974), ± compact inflorescence (Small, 1914; Jennings, 1917; Roig & Acuña, 1957; Southall & Hardin, 1974; Ebinger,

Table 1. **Comparative treatment of Cuban taxa of *Kalmia* by various botanists.** (PR = Pinar del Río; IP = Isle of Pines.)

botanist	"ericoides" variant	"simulata" variant	"aggregata" variant
Small (1914)	*K. ericoides* PR	—	*K. aggregata* IP
Jennings (1917)	*K. ericoides* PR	—	*K. aggregata* IP
Roig & Acuña (1957)	*K. ericoides* PR, IP	*K. simulata* IP	*K. aggregata* IP
Wood (1961)	*K. ericoides*	*K. ericoides*	*K. ericoides*
	(geographical distribution of variants not discussed)		
Southall & Hardin (1974)	*K. ericoides* PR, IP	*K. simulata* IP	*K. aggregata* PR, IP
Ebinger (1974)	*K. ericoides* var. *ericoides* PR	*K. ericoides* var. *ericoides* IP	*K. ericoides* var. *aggregata* IP
this study	*K. ericoides* var. *ericoides* PR	*K. ericoides* var. *aggregata* IP	*K. ericoides* var. *aggregata* IP

1974), and elongate calyx lobes (Southall & Hardin, 1974). Small (1914) considered the filaments to be glabrous, but Jennings (1917) correctly pointed out that the filaments of this taxon are slightly pubescent near the base, as are those of *K. ericoides*. This species is often stated to have larger leaves than either *K. ericoides* or *K. simulata* (see Small, 1914; Ebinger, 1974). Finally, *K. simulata*, a species described by Britton and Wilson (Britton, 1920), is typically characterized as having nearly glabrous to sparsely stipitate-glandular leaves but puberulent stems. Additional characters include the lax inflorescence (Britton, 1920; Roig & Acuña, 1957; Southall & Hardin, 1974; Ebinger, 1974) and short calyx lobes (Southall & Hardin, 1974; Ebinger, 1974). Although the interpretation of the geographical distribution of these three taxa has varied (see Table 1), a careful study of available herbarium specimens revealed that the plants fitting the general pattern of *K. ericoides* are

limited to Pinar del Río, while individuals agreeing with the descriptions of *K. aggregata* or *K. simulata* occur only on the Isle of Pines.

The range of variation and geographical correlation of the above mentioned characters (along with several additional characters) were surveyed through a study of herbarium specimens from throughout the range of this group. The results of this investigation are summarized in Table 2 and in the taxa descriptions.

The overall diversity in the Cuban taxa of *Kalmia* is comparable to that exhibited by many North American species of the genus (see Ebinger, 1974). The three described Cuban species differ only in a few indumentum characters, slight (and not too consistent!) differences in leaf and calyx lobe length, and inflorescence structure. Thus

Table 2. **Variation in selected morphological characters within the Cuban taxa of *Kalmia*.** (LC = long-celled hairs; GH = glandular-headed hairs)

character	"ericoides" variant	"simulata" variant	"aggregata" variant
unicellular hairs on stem	lacking or very sparse	± dense	± dense
multicellular hairs on stem	scattered GH; moderate to dense LC	scattered GH; sometimes a few LC	scattered to dense GH; often scattered LC
number of lvs. per cm on stem	ca. 4–25	ca. 10–25	ca. 9–25
unicellular hairs on adaxial leaf surface	lacking to sparse along midvein	lacking to sparse along midvein	moderate to dense (occasionally only sparse)
multicellular hairs on adaxial leaf surface	scattered GH and LC	scattered GH, sometimes also LC	scattered to dense GH, sometimes also LC
leaf length	(3–) 4–9 mm	(3–) 3.5–8.5 mm	5–14 mm
inflorescence	lax	lax	lax to compact
unicellular hairs on pedicels	lacking	sparse to dense	dense
unicellular hairs on abaxial surface of calyx lobes	lacking or with a few near apex or margin	moderate to dense throughout	dense throughout
calyx length	3–5 mm	3–4.5 mm	(3–) 4–6 mm
filaments	pubescent	pubescent	pubescent

all the Cuban populations of *Kalmia* are here considered as a single species: *Kalmia ericoides*. Within this assemblage the plants of the Isle of Pines were found to differ consistently from those of western Cuba in that their young stems are ± densely covered with unicellular hairs (*vs.* lacking to very sparsely covered with such hairs). Slight, but fairly consistent, differences in indumentum were also found on the pedicels, calyx lobes, and adaxial leaf surfaces (see key). *Kalmia ericoides sensu lato* thus is considered here to be composed of two geographical varieties—the first, var. *ericoides*, endemic to Pinar del Río, and the second, var. *aggregata*, endemic to the Isle of Pines. *Kalmia simulata* is included within *K. ericoides* var. *aggregata* because no combination of characters will unambiguously separate these two supposed taxa—all characters show extensive overlap (Table 2). The leaves of these Isle of Pines plants may lack unicellular hairs on the adaxial surface, be slightly pubescent along the midvein, slightly or moderately pubescent throughout, or densely pubescent; the multicellular pubescence varies from a sparse to dense covering of long to short-stalked glandular-headed hairs, sometimes with a few long-celled hairs intermixed. No morphological gap exists between the often nearly glabrous "simulata" variant and the densely unicellular-pubescent "aggregata" variant (see especially *Killip 45385* and *Ekman 12492*). In fact, both forms have been collected at the same locality (see *Killip 42882, Léon & Marie-Victorin 17852, 17853, 18857, Marie-Victorin & Alain 77, 77a*, all from Los Indios), and sometimes even mixed together on the same herbarium sheet. Clearly the *Kalmia* populations of this island (or at least the Los Indios area) are variable in leaf pubescence. Continuous variation in leaf length, internode length, compactness of inflorescence, and calyx length is also present.

Ebinger (1974) considered *Kalmia simulata* to be a synonym of *Kalmia ericoides* var. *ericoides* based upon characters of indumentum, leaf and calyx lobe length, and compactness of the inflorescence. However, as indicated in Table 2 (and in discussion above) these characters do not support Ebinger's placement of these plants. Thus the basic dichotomy within the Cuban Kalmias is between those populations of Pinar del Río which have young stems essentially lacking unicellular hairs but with a moderate to dense covering of long-celled hairs and scattered glandular-headed hairs, and those of the Isle of Pines which have stems with a ± dense covering of unicellular hairs along with a sparse to dense covering of short to

long-stalked glandular-headed hairs and often a few long-celled hairs. A single plant *(Marie-Victorin & Alain 77a)* from the Isle of Pines completely lacks unicellular hairs on the young twigs. However, this plant grew together with densely pubescent plants (see *Marie-Victorin & Alain 77*) and can be identified by its leaf indumentum.

Keys and descriptions of the Cuban taxa of *Kalmia* follow.

Kalmia ericoides Wright ex Griseb. Cat. Pl. Cubensium **51**. 1866.

An evergreen erect to decumbent-spreading, sparsely branched shrub to 1 (–1.4) m tall with a thickened or burl-like stem just below soil surface; frequently sprouting from base after fire or disturbance. Bark of larger branches dark brown and longitudinally furrowed. Twigs terete, light gray to reddish, slender to stout, densely covered with unicellular hairs to lacking such hairs, sparsely to densely covered with multicellular, multiseriate, short- to long-stalked glandular-headed hairs, and lacking to densely covered with multicellular, multiseriate, long-celled hairs. Buds minute, to 0.3 mm long, densely covered with glandular-headed and long-celled hairs. Leaves alternate and sparsely to densely distributed along stem (ca. 4–25 (–30) leaves per cm); blade linear to ovate, (3–) 3.5–14 mm long, 0.5–3 (–4) mm wide, coriaceous; apex acute; base cuneate to rounded; margin strongly revolute; adaxial surface densely covered with unicellular hairs to lacking such hairs, very sparsely to densely covered with short- to long-stalked glandular-headed hairs, and lacking to sparsely covered with long-celled hairs; abaxial surface sparsely to densely covered with unicellular hairs, occasionally such hairs completely lacking, with scattered short- to long-stalked glandular-headed hairs and sometimes long-celled hairs; petiole essentially lacking to 1.5 mm long with a unifacial vascular bundle. Flowers 5-merous, solitary (or occasionally in fascicles or short racemes), in the axils of leaves or bract-like leaves at ends of branches, thus forming a pseudoterminal cluster. Pedicels 4–14 mm long, densely covered with unicellular hairs to lacking such hairs, with scattered glandular-headed hairs and sometimes also long-celled hairs; bracteoles two, opposite and basal, ovate-triangular to narrowly triangular, 1–3 mm long, with unicellular hairs and glandular-headed hairs. Calyx lobes narrowly triangular to ovate-triangular, 3–6 mm long, 0.8–2.3 mm wide, green, with slightly

acuminate to acute apices, tardily deciduous in fruit; adaxial surface densely covered with unicellular hairs to lacking such hairs, with or without scattered glandular-headed and/or long-celled hairs; abaxial surface with a few unicellular hairs near apex to densely covered with such hairs, with scattered glandular-headed hairs, sometimes also long-celled hairs. Corolla with a short cylindrical tube extending into a shallowly lobed and rotate limb, with saccate depressions in which the anthers are held under tension, 6–12 mm long, 8–17 mm wide, white to pink; adaxial surface sparsely covered with unicellular hairs toward base (tubular portion); abaxial surface with glandular-headed and sometimes also long-celled hairs, occasionally

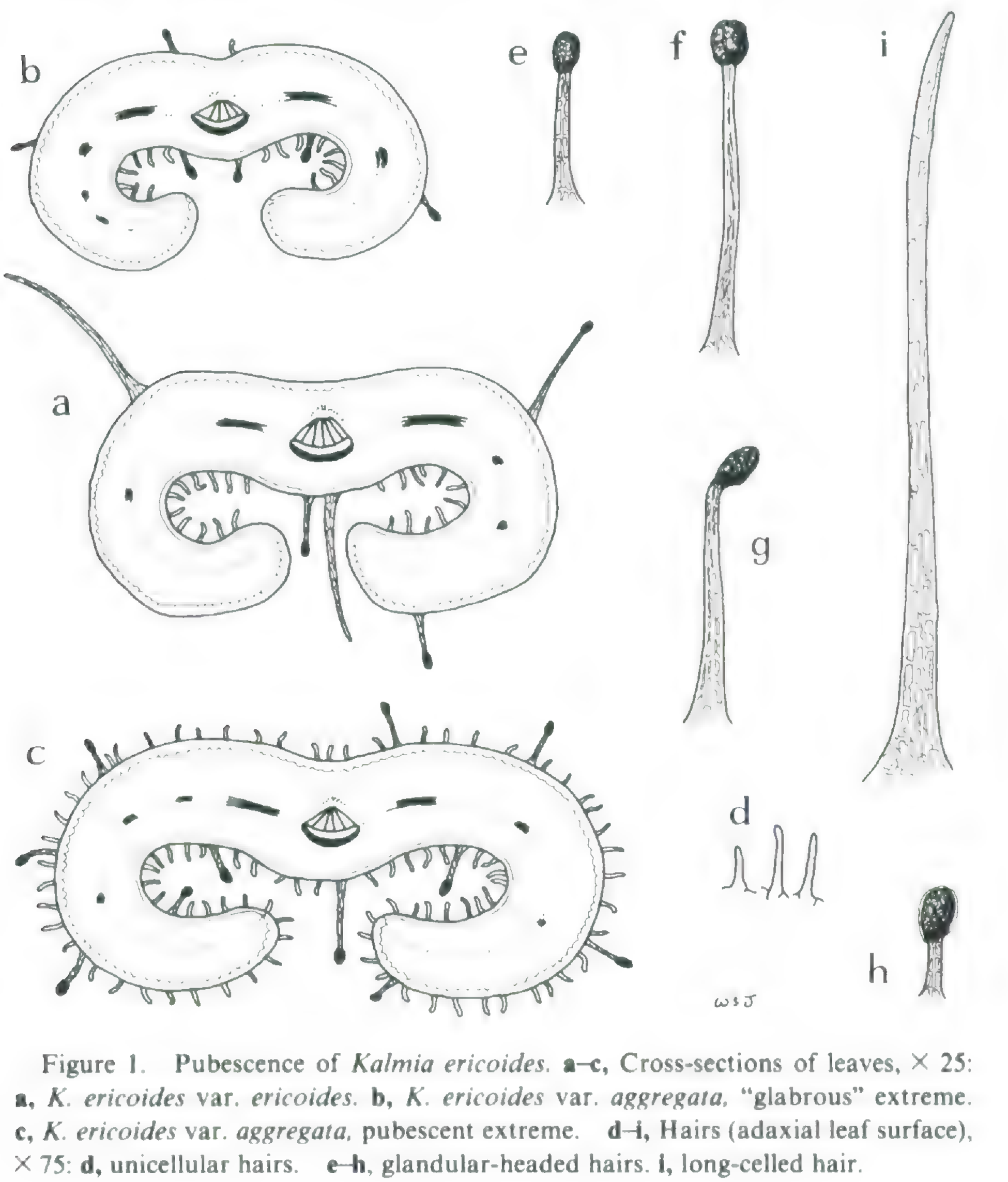

Figure 1. Pubescence of *Kalmia ericoides*. **a–c,** Cross-sections of leaves, × 25: **a,** *K. ericoides* var. *ericoides*. **b,** *K. ericoides* var. *aggregata,* "glabrous" extreme. **c,** *K. ericoides* var. *aggregata,* pubescent extreme. **d–i,** Hairs (adaxial leaf surface), × 75: **d,** unicellular hairs. **e–h**, glandular-headed hairs. **i,** long-celled hair.

also with a few unicellular hairs. Filaments sparsely to moderately covered with unicellular hairs near base and glabrous above, 3–5 mm long; anthers ovoid, 0.7–1.2 mm long, opening by large, ± terminal, slit-like pores; pollen released in tetrads with viscid strands. Ovary with axile placentation and centrally located, bi-lobed placentae; style 3.5–7 mm long. Fruit a septicidal capsule, subglobose to ovoid, 1.7–3 mm long, 2–4 mm wide, sparsely to densely covered with glandular-headed hairs, sometimes also with a few unicellular hairs. Seeds brown, ovoid, 0.4–0.7 mm long, the testa of slightly elongated and minutely pitted cells, not extending past the ends of the seed; embryo minute.

KEY TO VARIETIES

1. Stems lacking unicellular hairs to very sparsely unicellular-pubescent; pedicels lacking unicellular hairs; abaxial surface of calyx lobes lacking unicellular hairs or with only a few near apex or along margin; adaxial surface of leaves lacking unicellular hairs to sparsely covered with such hairs along mid-vein; [Pinar del Río] ..... var. *ericoides*
1. Stems ± densely covered with unicellular hairs; pedicels very sparsely to densely covered with unicellular hairs; abaxial surface of calyx lobes moderately to densely covered with unicellular hairs throughout; adaxial surface of leaves lacking unicellular hairs to densely covered with such hairs; [Isle of Pines] ..... var. *aggregata*

Kalmia ericoides Wright ex Griseb. var. **ericoides**

Chamaedaphne ericoides (Wright ex Griseb.) Kuntze, Rev. Gen. Pl. **2**: 388. 1891. *Kalmiella ericoides* (Wright ex Griseb.) Small, North Amer. Fl. **29**: 54. 1914. TYPE: Cuba, Pinar del Río: Guane, near La Grifa, *C. Wright 2199* (HOLOTYPE: GOET, not seen; ISOTYPES: GH, MO!, NY (3 sheets)!, US).

Stems lacking unicellular hairs or very sparsely covered with such hairs, with a moderate to dense covering of long-celled hairs and glandular-headed hairs. Leaves (3–) 4–9 mm long, 0.5–1.7 (–3) mm wide; adaxial surface lacking unicellular hairs or only sparsely covered with such hairs on mid-vein (especially near base), with scattered glandular-headed hairs and conspicuous, long-celled hairs (especially along margin near base). Pedicels lacking unicellular hairs, usually longer than subtending leaves, thus giving inflorescence an open appearance. Calyx lobes 3–5 mm long; abaxial sur-

face with a few unicellular hairs near apex and along margin, with scattered glandular-headed and long-celled hairs. Capsules lacking unicellular hairs. (Figure 1; see also Southall & Hardin, 1974).

inflorescence a compact to open appearance. Calyx lobes 3–6 mm long; abaxial surface moderately to densely (or occasionally only sparsely) covered with unicellular hairs throughout, with a sparse to dense covering of glandular-headed hairs, often also with long-celled hairs. Capsule with or without unicellular hairs. (Figure 1; see also Jennings, 1917; Marie-Victorin & Léon, 1944; Roig & Acuña, 1957; Southall & Hardin, 1974.)

DISTRIBUTION AND ECOLOGY. Cuba, Isle of Pines (Figure 2), in whitesand savannas and pinelands (dominants: *Pinus tropicalis, P. caribaea, Colpothrinax wrightii,* and *Acoelorraphe wrightii*); for detailed discussion of vegetation along with lists of characteristic species see Jennings (1917), Marie-Victorin & Léon (1944), Alain (1946). Flowering from November through May.

DISTRIBUTION AND ECOLOGY. Cuba, prov. Pinar del Río (Figure 2), in white-sand savannas; associated species briefly discussed by Marie-Victorin & Léon (1944). Flowering from November through May (June).

REPRESENTATIVE SPECIMENS: Cuba, prov. Pinar del Río. Sabanalamar, El Sábalo, *Bro. Alain 1326* (GH, US); Arroyo Mantua, Damuji, near Rincon del Prado, *Ekman 11024* (NY); La Grifa, Laguna Larga, *Ekman 18165* (NY, US); Laguna de Alcatraz Grande, Remates de Guane, *Bros. Léon & Marie-Victorin 18706* (GH, US).

Kalmia ericoides Wright ex Griseb. var. **aggregata** (Small) Ebinger, Rhodora **76**: 389. 1974.

Kalmiella aggregata Small, North Amer. Fl. **29**: 54. 1914. *Kalmia aggregata* (Small) Copeland, Amer. Midl. Nat. **30**: 571. 1943. TYPE: Cuba, Isle of Pines: Los Indios, 17 May 1910, *Jennings 324* (HOLOTYPE: NY!; ISOTYPE: MO!).

Kalmiella simulata Britton & Wilson, Mem. Torrey Bot. Club **16**: 93. 1920. *Kalmia simulata* (Britton & Wilson) Southall, Jour. Elisha Mitchell Sci. Soc. **90**: 22. 1974. TYPE: Cuba, Isle of Pines, vicinity of Los Indios, 13 Feb. 1916, *Britton, Britton & Wilson 14205* (HOLOTYPE: NY!).

Stem ± densely covered with unicellular hairs, with sparse to dense covering of glandular-headed hairs and often with long-celled hairs. Leaves (3–) 3.5–14 mm long, 0.5–3 (–4) mm wide; adaxial

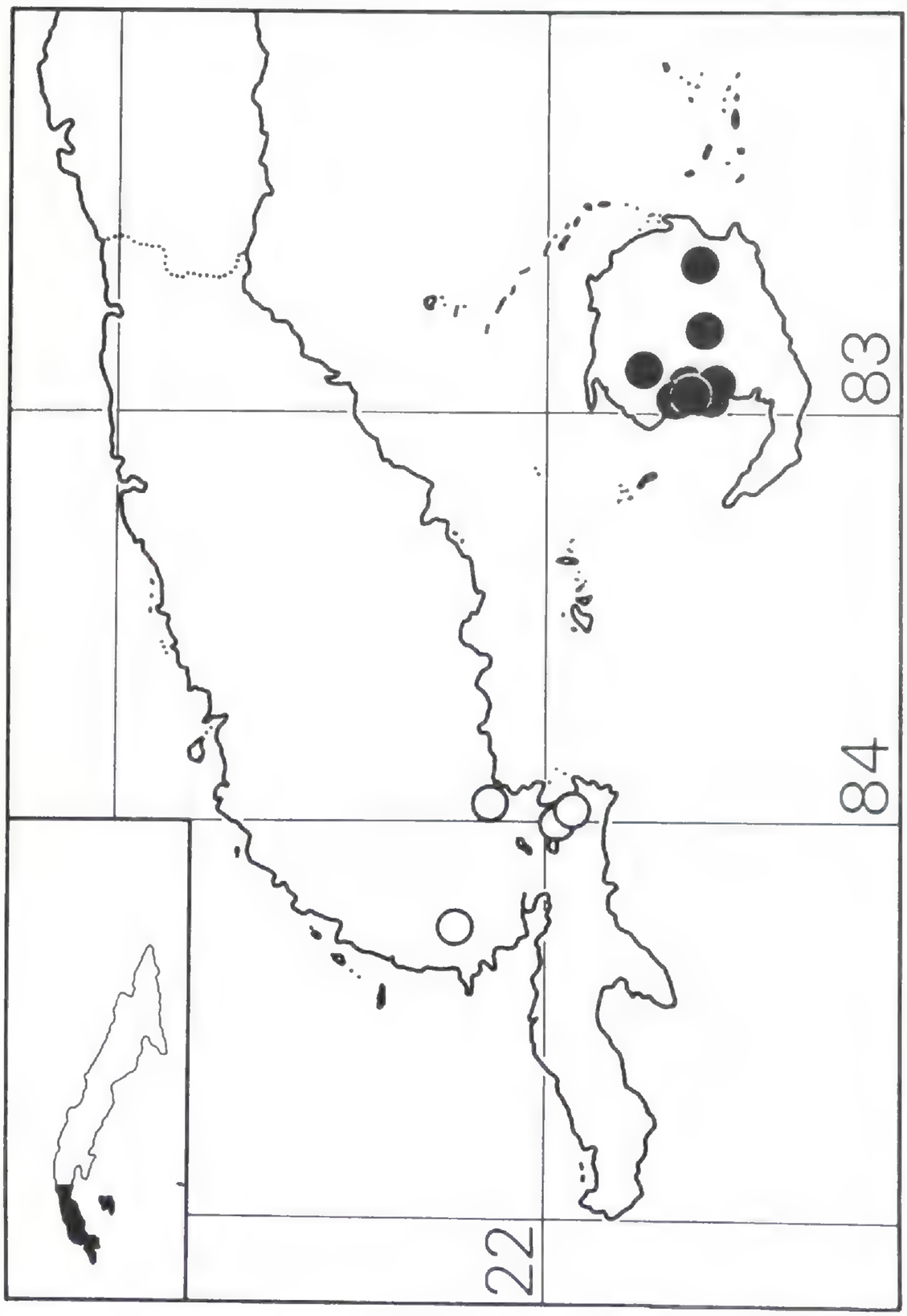

Figure 2. Distribution of *Kalmia ericoides* var. *ericoides* (circles) and *K. ericoides* var. *aggregata* (dots).

surface lacking to densely covered with unicellular hairs throughout, with sparse to dense covering of glandular-headed hairs and sometimes a few long-celled hairs. Pedicels very sparsely to densely covered with unicellular hairs, variable in length, thus giving the

REPRESENTATIVE SPECIMENS: Cuba, Isle of Pines: San Pedro, *Britton, Britton & Wilson 14146* (F, GH, MO, NY, US); Santa Bárbara, Westport, *Ekman 12096* (NY); Loma Dagnillo, *Ekman 12492* (NY); Los Indios, *Killip 42882* (F, GH, NY, US); Playa Roja, *Killip 43001* (GH, NY, US); between Mina de Oro and Playa del Soldado, *Killip 45385* (GH); Los Indios, *Bros. Léon & Marie-Victorin 17852* (GH, US), *17853* (GH), *18857* (GH, US); Los Indios, *Bros. Marie-Victorin & Alain 77* (GH, NY, US), *77a* (US).

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LITERATURE CITED

ALAIN, HNO. (= A. H. LIOGIER) 1946. Notas taxonomicas y ecologicas sobre la flora de Isla de Pinos. Contr. Ocas. Museo Hist. Nat. Colegio "De La Salle" **7**: 13–106.

BRITTON, N. L. 1920. Description of Cuban plants new to science. Mem. Torrey Bot. Club **26**: 57–118.

EBINGER, J. E. 1974. A systematic study of the genus *Kalmia* (Ericaceae). Rhodora **76**: 315–398.

JENNINGS, O. E. 1917. A contribution to the botany of the Isle of Pines, Cuba. Ann. Carnegie Museum **15**: 19–290.

MARIE-VICTORIN, FRÈRE & FRÈRE LÉON. 1944. Itinéraires botaniques dans l'Ile de Cuba. Contr. Inst. Bot. Univ. Montréal **50**: 11–410.

ROIG, J. T. & J. ACUÑA. Ericaceae *in:* Hno. Léon & Hno. Alain. 1957. Flora de Cuba, vol. 4. Contr. Ocas. Museo Hist. Nat. Colegio "De La Salle" **10**: 91–106.

SMALL, J. K. 1914. Ericaceae. North American Flora **29**: 33–102.

SOUTHALL, R. M. & J. W. HARDIN. 1974. A taxonomic revision of *Kalmia* (Ericaceae). Jour. Elisha Mitchell Sci. Soc. **90**: 1–23.

WOOD, C. E., JR. 1961. The genera of Ericaceae in the Southeastern United States. Jour. Arnold Arbor. **42**: 10–80.

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THE NATIONAL HISTORICAL DISTRIBUTION OF *PLATANTHERA PERAMOENA* (A. GRAY) A. GRAY (ORCHIDACEAE) AND ITS STATUS IN OHIO

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ABSTRACT

An updated county distribution map of *Platanthera peramoena* was made utilizing data from state natural heritage programs and similar organizations. Herbarium and field surveys were conducted by Ohio Division of Natural Areas and Preserves staff for Ohio localities of the species. These studies identified 41 sites of *P. peramoena* in Ohio, and habitats were identified where new populations are likely to be found.

In Ohio, *P. peramoena* is a plant of wet acidic soils on the Illinois till plain and in the unglaciated Allegheny plateau. While not common in the state it is not in imminent danger of extirpation.

Platanthera (Habenaria) peramoena (A. Gray) A. Gray (Purple Fringeless Orchid) was placed under review as a threatened species by the U.S. Fish and Wildlife Service (the Service), as a result of the 1974 Smithsonian Institution's Report on endangered and threatened species of the United States. This report was requested by Congress in the Endangered Species Act of 1972 (Public Law 93-205, Approved Dec. 29, 1973). Subsequent to this proposal, the Service received additional information on this species from various states, and on December 15, 1980, *P. peramoena* was formally withdrawn from consideration because it was found to be more widespread than was previously believed (U.S. Fish and Wildlife Service, 1980).

The formal review of this and other species by the Service focused attention on their possible rarity. Partly as a result of this listing, *Platanthera peramoena* was included on many newly developing state and regional rare plant lists. Attention was further focused when the Service contracted various state natural heritage programs and other similar agencies to study the status of plants listed within their respective states. The Ohio Department of Natural Resources, Division of Natural Areas and Preserves, manager of the Ohio Natural Heritage Program, entered into a formal two-year study of this species.

METHODS

Ohio records of *P. peramoena* were obtained from the Ohio Natural Heritage Program data base. These records were obtained from a survey of 26 Ohio herbaria and the U.S. National Herbarium. Field work was planned utilizing these records as guides to previous occurrences of the species. When the locational data was specific enough, the old records were field checked.

The following organizations were consulted to obtain updated distributional information outside of Ohio:

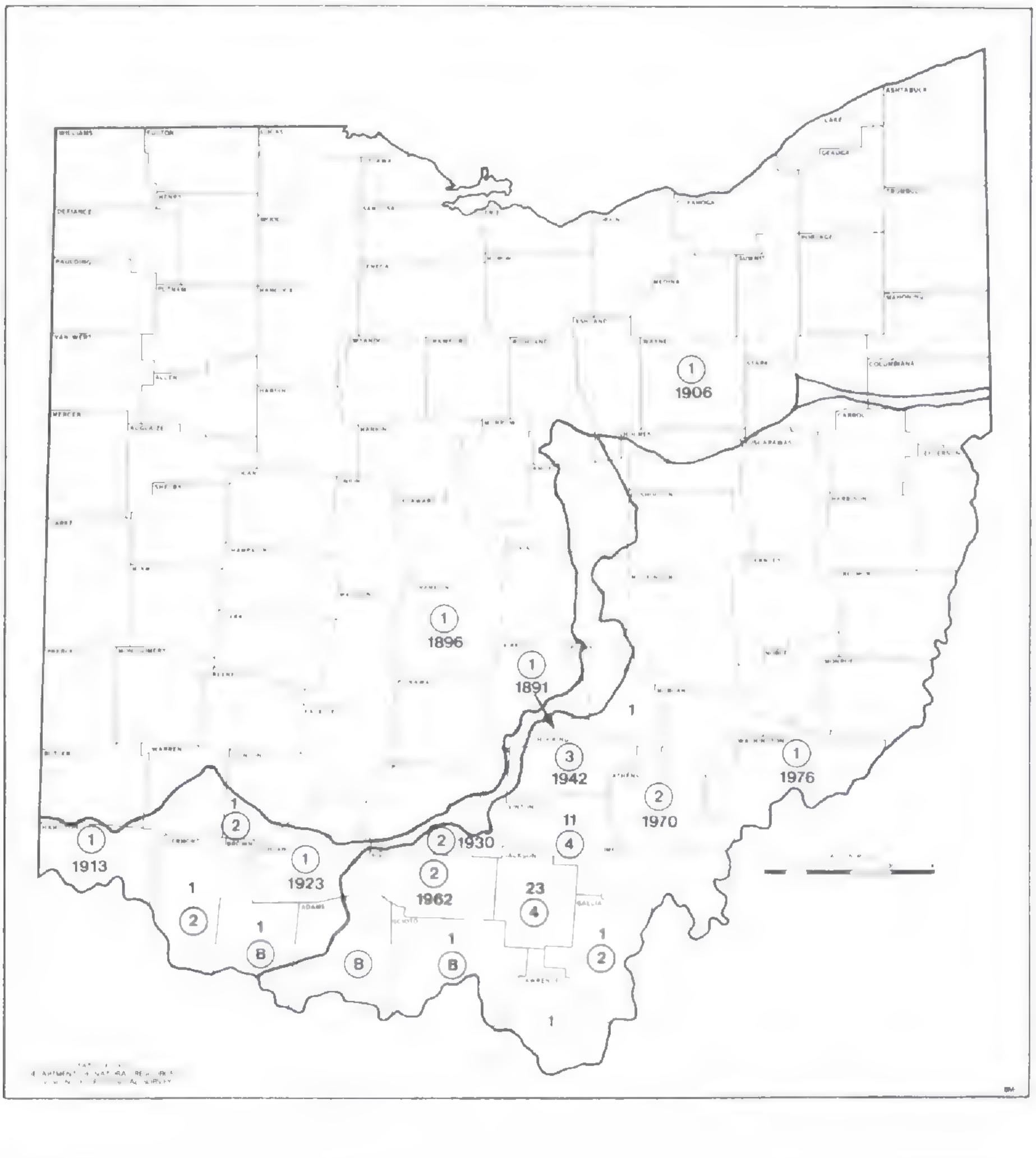
The Arkansas Natural Heritage Inventory
The Indiana Natural Heritage Program
The Illinois Department of Conservation
The Kentucky Nature Preserves Commission
The Maryland Natural Heritage Program
The Mississippi Natural Heritage Program
The Missouri Department of Conservation
The Conservation and Environmental Studies Center, Inc. of New Jersey
The North Carolina Natural Heritage Program
The South Carolina Heritage Trust Program
The Tennessee Natural Heritage Program
The Tennessee Valley Authority Regional Natural Heritage Project
The Virginia Natural Diversity Information Program
The Western Pennsylvania Conservancy
The West Virginia Natural Heritage Program

In addition, recent state and regional floras (references 3, 9, 10, 11, 16, 19, 21, 25, 27, 30, 33), state endangered species publications (4, 12, 18, 20, 26, 31, 34), and regional treatments of orchids (7, 8, 13, 14, 23, 24), were consulted for relevant information.

RESULTS

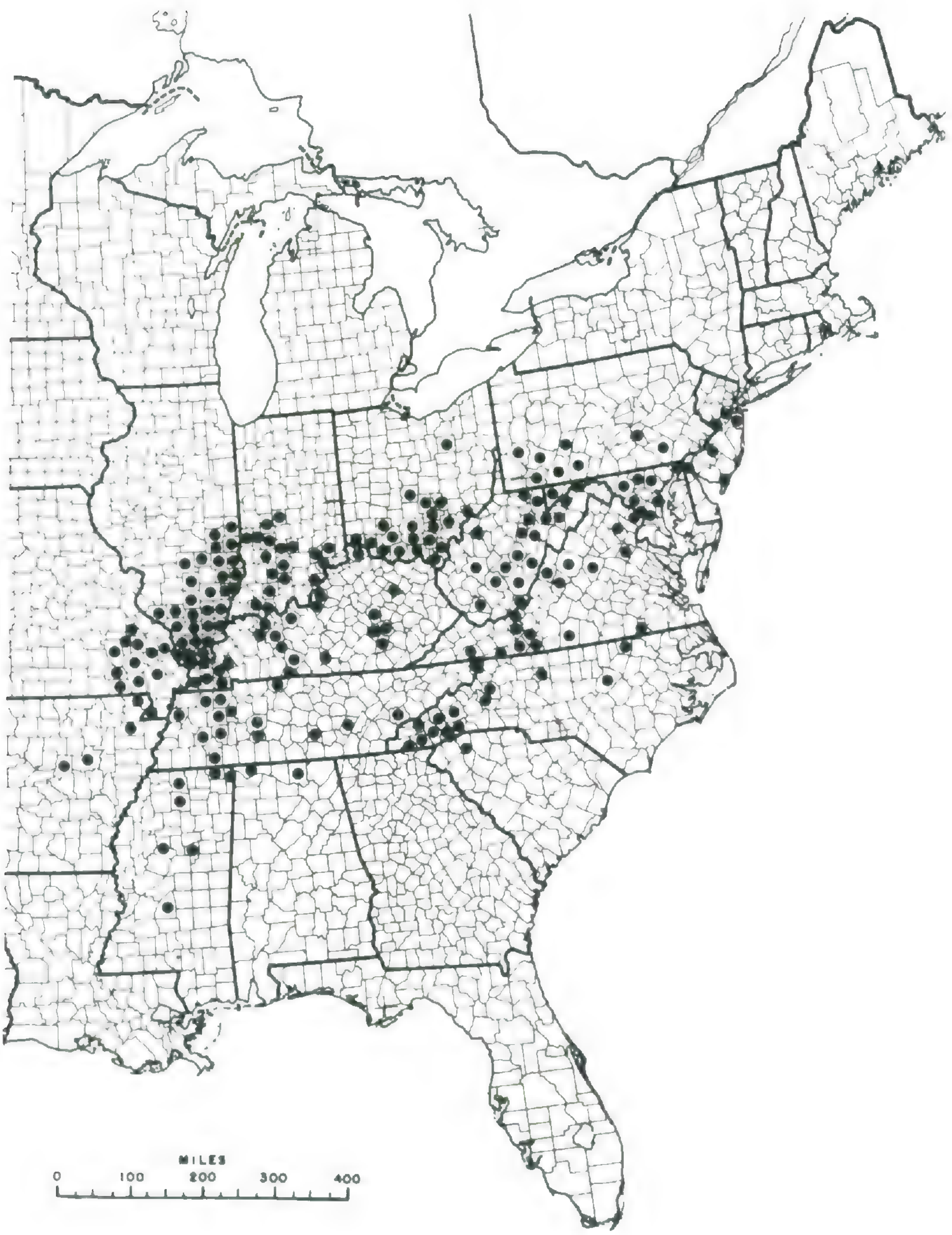
Total Distribution

The only published county dot map of *Platanthera peramoena* for its entire range is that of Ayensu (1974). Literature references and heritage information added new records. New maps were made for the distribution of this species in Ohio (Map 1), and for its national historical range (Map 2).



Map 1. Ohio distribution of *Platanthera peramoena*. The lines to the north and west are the limits of Wisconsin glaciation. The numbers in the counties represent the number of stations reported in the counties. Uncircled numbers represent populations located since 1978; circled numbers represent populations not relocated since this date. The date is the most recent record for the county. B refers to a reference from Braun (1967).

Platanthera peramoena is often listed or diagrammed as occurring in New York. This is apparently based on House (1924). Zenkert (1934), however, pointed out that this report was due to an error in transcription, *P. peramoena* being substituted for *P. fimbriata*. Sheviak (personal communication, 1981) checked the New York State Museum (NYS), and found no New York specimens of *P. peramoena*. Another possible source of error may have been misidentifica-



Map 2. Total historical distribution of *Platanthera peramoena*.

tions with *P. psycodes* or *P. grandiflora*. Both of these errors were found in old New York specimens deposited at The Ohio State University (OS).

Platanthera peramoena is also often listed or diagrammed as occurring in Georgia. Correll (1950) lists it for Georgia, citing S. B. Buckley as the collector. Duncan and Kartesz (1981) also list it for Georgia. Many of Buckley's labels read "in montibus Carolinae et Georgiae." We have records from 26 Ohio herbaria, and sent inquiries to the New York State Museum (NYS), the University of Georgia (GA), the U.S. National Herbarium (US), the Missouri Botanical Gardens (MO), the Philadelphia Academy of Natural Sciences (PH), and Yale University (Y). Correll suggested the last four herbaria, as he obtained many of his records there. We have found no Georgia record for this species. If it exists in another herbarium, it can only doubtfully be ascribed to Georgia if the locational data is like the one above.

Status in Ohio

Over the past three years, the Division of Natural Areas and Preserves field staff has found many new sites for *Platanthera peramoena*. In many cases, old records have been relocated. Post-1978 populations are now known from 41 locations in nine counties. Herbarium specimens exist from ten other counties. In addition, Braun (1967) maps an Adams County record. We were not able to locate any specimen from this county, or pre-1967 specimens from Brown and Scioto counties.

In Ohio, *Platanthera peramoena* grows in areas that are wet in the spring, but which may become droughty later in the year. It grows most often in full sun or partial shade, and is occasionally found in deep shade. The most common habitat is an open swampy area or low wet depression, and in such situations populations can include scores of individuals. It is infrequent on exposed moist slopes, and in such situations both individuals and populations are generally smaller. One individual was found in an area that was extensively trampled and grazed by cattle. The most vigorous populations are known from moderately disturbed sites, such as periodically mowed or lightly grazed wet fields, or recently logged swampy areas.

All presently known populations occur on seasonally wet acidic soils of the unglaciated Allegheny Plateau, or on the highly leached acidic soils of the Illinois Till Plain, south of the Wisconsin Till

Plain border. Swampy habitats on the unglaciated Allegheny Plateau occur on lacustrine silts and clays deposited in many of the deeper pre-glacial valleys of the Teays River system and its tributaries. These lacustrine deposits were laid down during a damming of the Teays River by the Kansan or pre-Kansan glacier, forming a vast lake, which innundated the lower elevations of much of southern Ohio and adjacent West Virginia and Kentucky (Stout et al., 1943).

DISCUSSION

Platanthera peramoena is not presently an exceptionally rare plant in Ohio. There are a number of reasons, however, which may explain why it is not commonly seen and collected. First, it has a rather brief blooming period, and when not in bloom it is very inconspicuous among the surrounding tall vegetation. Most Ohio records are from mid-July to mid-August, but the blooming period in any one year lasts only about two weeks, and it quickly goes out of bloom. Second, even at a short distance, it is very similar in appearance to *Phlox paniculata* L. and *Phlox maculata* L. The size, general form of the inflorescence, flower color, and habitat of these plants are similar, and *Platanthera peramoena* is often found growing with them. These phloxes are very common and widespread in Ohio, and *P. peramoena* is easily overlooked. Third, many populations of *P. peramoena* occur in swampy, weedy habitats that are not particularly pleasant to explore. Fourth, and perhaps of greatest importance, populations do not bloom every year. This phenomenon is known for many orchid species and dramatic changes in number of blooming plants per population have been noted for *P. flava* (Buker, 1980) and *P. peramoena* (Henry & Buker, 1955; Henry, Buker, & Pearth, 1975). The reason for these yearly changes is not understood, but there are various possible explanations. Case (1964), Sheviak (1974), and Stoutamire (1974) point out that disturbance can cause rapid changes in wild orchid populations. This rapid colonization could come about by the reseeding of an area from an outside source, well documented for other orchid species (Stoutamire, 1974). Another possible reason for shifts in the population size may be the delayed germination of orchid seeds, but this is not well documented. Another reason is the possible periodic shift of the plant from an autotrophic to a temporary heterotrophic state. This

phenomenon is known for *Triphora trianthophora* (Sw.) Rydb., and Sheviak (1974) has observed it for other orchid species under horticultural conditions. Case (1964), however, doubts that this is a cause for population shifts in nature. This autotrophic to heterotrophic shift might very possibly be triggered by environmental conditions that are as yet very poorly understood. Sheviak (1964) points out that these conditions may operate on the mycorrhizae of the orchid. Clearly, this is a fertile area for research.

The general distribution of *Platanthera peramoena* on the Illinois Till Plain of Ohio parallels the situation in Illinois, where a similar Wisconsinan-Illinoian edaphic transition exists. Similar wet acidic soils developed on silts of lacustrine origin in southeastern Ohio. The occurrences of *P. peramoena* in Franklin County (one record, 1896-"Clintonville"), and in Wayne County (one record, 1906-county only mentioned) are apparently disjunct. Soil surveys of Franklin County (McLoda & Parkinson, 1980) and of Wayne County (Bureau & Scherzinger, in press) were checked to see if there were any areas that might be favorable for the growth of this species. There were indeed many sites in these counties that seemed to have similar conditions of moisture and acidity. While the majority of Wisconsinan-age soils in Ohio are generally calcareous, there are also many locally wet acidic soils. It is not understood why *P. peramoena* apparently has not colonized them.

Platanthera peramoena has varying degrees of rarity in different parts of its range. It is believed extirpated from Delaware (Tucker et al., 1979), South Carolina (pers. comm., SC Heritage staff), and possibly New Jersey (Snyder & Vivian, 1981). Reveal and Broome (1981) believe it to be in danger of extirpation from Maryland due to a combination of habitat modification and overcollecting. It is listed as a "special concern" species (due to vulnerability of its habitat) in Alabama (Freeman et al., 1979), Tennessee (pers. comm., TN Heritage staff), and Virginia (pers. comm., VA Heritage staff). Pennsylvania lists it as threatened, but it is widespread throughout the southern part of the state (Wiegman, 1979). It recently has been found to be much more widespread than was originally believed in Kentucky (pers. comm., KY Heritage staff), and West Virginia, where it has been taken off the West Virginia state list (pers. comm., WV Heritage staff). Sheviak (1974) mentions it as widespread in southern Illinois, and believes it to be the most common member of its genus in southern Illinois.

In Ohio, *Platanthera peramoena* is not in imminent danger of extirpation. Populations are believed to have disappeared after cultivation of an area, and drainage of the habitat would very likely eliminate populations, but habitats exist in southern Ohio that support apparently healthy populations. We believe that moderate disturbance has increased its numbers in the state and that there are many as yet undiscovered stations for it in southern Ohio.

The increasing awareness of endangered habitats and species is stimulating the development of rare species lists and their refinement through selective and planned field surveys. Many lists are initially based on randomly collected herbarium data. Data bases of the occurrences of these species are under various stages of development in different states, and new records are being obtained by these selective field surveys. Studies of species being considered for federal listing, such as *Platanthera peramoena*, could especially benefit from heritage program data. They are studied throughout their range, and not just in peripheral areas, where they are considered rare. The information gained through natural heritage program surveys will prove to be rich sources of data in future years.

ACKNOWLEDGMENTS

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LITERATURE CITED

1. Ayensu, E. S. 1975. Endangered and threatened orchids of the United States. Am. Orchid Soc. Bull. **44**: 384–394.
2. _____. & R. A. DeFilipps. 1978. Endangered and threatened plants of the United States. Smithsonian Institution World Wildlife Fund, Inc. Washington, D.C. 403 p.
3. Braun, E. L. 1967. The Monocotyledonae [of Ohio]: Cat-tails to orchids. With Gramineae by C. G. Weishaupt. Ohio State University Press, Columbus, Ohio. 464 p.

4. Broome, C. R., J. L. Reveal, A. O. Tucker, & N. H. Dill. 1979. Rare and endangered vascular plants of Maryland. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts. 64 p.
5. Buker, W. 1980. Population explosions among the orchids. Castanea **45**: 144–145.
6. Bureau, M. F., & R. J. Scherzinger. (to be published in 1983). Soil survey of Wayne County, Ohio. USDA Soil Conservation Service, U.S. Government Printing Office, Washington, D.C.
7. Case, F. W., Jr. 1964. Orchids of the western Great Lakes. Cranbook Institute of Science, Bloomfield Hills, Michigan. 147 p.
8. Correll, D. S. 1950. Native orchids of North America north of Mexico. Chronica Botanica Company, Waltham, Massachusetts. 399 p.
9. Cusick, A. W., & G. M. Silberhorn. 1977. The Vascular Plants of Unglaciated Ohio. Ohio Biol. Surv. Bull. (New Series) Vol. **5**, No. 4. 157 p.
10. Deam, C. C. 1940. Flora of Indiana. Burford Printing Co., Indianapolis. 1236 p.
11. Duncan, W. H., & J. T. Kartesz. 1981. Vascular Flora of Georgia. The University of Georgia Press, Atlanta. 143 p.
12. Freeman, J. D., A. S. Causey, J. W. Short, & R. R. Haynes. 1979. Endangered, threatened, and special concern plants of Alabama. Department of Botany and Microbiology, Agricultural Experiment Station, Departmental Series No. **3**, Auburn University, Auburn, Alabama. 25 p.
13. Henry, L. K., & W. E. Buker. 1955. Orchids of Western Pennsylvania. Ann. Carnegie Mus. **33**: 299–346.
14. _____, _____, & D. L. Pearth. 1975. Western Pennsylvania Orchids. Castanea **40**: 93–168.
15. House, H. D. 1924. Annotated list of the ferns and flowering plants of New York State. New York State Museum Bulletin, The University of the State of New York. 759 p.
16. Lowe, E. N. 1921. Plants of Mississippi. A list of flowering plants and ferns. Mississippi State Geological Survey, Bulletin **17**. 292 p.
17. McLoda, N. A., & R. J. Parkinson. 1980. Soil Survey of Franklin County, Ohio. USDA Soil Conservation Service, U.S. Government Printing Office, Washington, D.C. 188 p. + 69 pl.
18. Massey, J. R., & R. D. Whetstone. 1978. Threatened and endangered vascular plants of western North Carolina. Southeastern Forest Experiment Station, Highlands Biological Station, Cooperator.
19. Mohlenbrock, R. H., & D. M. Ladd. 1978. Distribution of Illinois vascular plants. Southern Illinois University Press, Carbondale and Edwardsville. 282 p.
20. Porter, D. M. 1979. Rare and endangered vascular plant species in Virginia. U.S. Fish and Wildlife Service.
21. Radford, A. E., H. E. Ahles, & C. R. Bell. 1964. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill, North Carolina. 1183 p.
22. Reveal, J. L. & C. R. Broome. 1981. Minor nomenclatural and distributional notes on Maryland vascular plants with comments on the state's proposed endangered and threatened species. Castanea **46**: 50–82.

23. Reed, C. F. 1964. Orchidaceae of Maryland, Delaware, and the District of Columbia. Castanea **29**: 77–109.
24. Sheviak, C. J. 1974. An Introduction to the ecology of the Illinois Orchidaceae. Illinois State Museum, Scientific Papers **XIV**. Springfield, Illinois. 89 p.
25. Smith, Edwin B. 1978. An atlas and annotated list of the vascular plants of Arkansas. University of Arkansas Bookstore, Fayetteville, Arkansas. 592 p.
26. Snyder, D. B., & V. E. Vivian. 1981. Rare and endangered vascular plant species in New Jersey. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts. 98 p.
27. Steyermark, J. A. 1977. Flora of Missouri. The Iowa State University Press, Ames, Iowa. 1728 p.
28. Stout, W., K. Ver Steek, & G. F. Lamb. 1943. Geology of water in Ohio. Bull. **44**, Ohio Division of Geological Survey. 694 p.
29. Stoutamire, W. P. 1974. Terrestrial orchid seedlings. *In:* Withner, The Orchids, Scientific Studies. John Wiley and Sons, New York. p. 101–128.
30. Strausbaugh, P. D. & E. L. Core. 1970. Flora of West Virginia. Part 1, Ed. 2. West Virginia University Bulletin, Series **70**, No. 7–2. 273 p.
31. Tucker, A. O., H. H. Dill, C. R. Broome, C. E. Phillipps, & M. J. Maciarello. 1979. Rare and endangered vascular plant species in Delaware. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts. 89 p.
32. U. S. Fish & Wildlife Service. 1980. Endangered and threatened wildlife and plants: Review of plant taxa for listing as endangered or threatened species. Federal Register **45**: No. 242.
33. Wherry, E. T., J. M. Fogg, Jr. & H. A. Wahl. 1979. Atlas of the flora of Pennsylvania. Morris Arboretum of the University of Pennsylvania. 390 p.
34. Wiegman, P. G. 1979. Rare and endangered vascular plant species in Pennsylvania. U.S. Fish and Wildlife service. 94 p.
35. Zenkert, C. A. 1934. The flora of the Niagara frontier region. Ferns and flowering plants of Buffalo, New York, and vicinity. Bull. Buffalo Soc. Nat. Sci. **16**. 313 p.

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WIND DISPERSAL OF SOME NORTH AMERICAN SPECIES OF *ANDROPOGON* (GRAMINEAE)

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Abstract: The plumed diaspores of the genus *Andropogon* are wind-dispersed. The dispersibility of Andropogons helps account for their success as colonizers both in their infestation of appropriate sites and their spread to newly available sites. The wind may also be responsible for the long-distance dispersal of *A. bicornis* L. from the Caribbean to southern Florida. This is the first record of this widespread New World taxon in the United States.

Many species of the cosmopolitan genus *Andropogon* are remarkably successful colonizers. Wherever there is full sun and in all but the poorest and driest of soils, they rapidly form large, dense populations. Some species usually grow away from frequent disturbance of the habitat by man and rely upon fire and other natural phenomena for an open canopy. Others are of limited range in man-made habitats like roadsides and old fields. The commonest species, such as *A. virginicus* L., tend to dominate all other vegetation in early stages of secondary succession (Keever, 1950; Golley, 1965; Bazzaz, 1975). The colonizing success of Andropogons comes, at least in part, from their dispersibility.

Andropogons flower at the end of the first or second year of growth. The number of flowers per stem varies from as few as 100 in *Andropogon gyrans* Ashe (long incorrectly known as *A. elliottii* Chapman) to as many as 10,000 in *A. glomeratus* (Walter) B.S.P. The number of stems per individual may be as high as 60. Fruit set depends upon the favorability of the habitat for growth, the extent of insect predation and other natural adversities (e.g. infestation by the smut *Sorosporium*), which vary considerably and can reduce fruit set greatly as in other grasses (Roos & Quinn, 1977). The caryopsis is small (1–4 mm long and less than 0.5 mm in diameter) and light (0.2–0.9 mg). It remains within the spikelet after maturation. Dispersal of the fruit begins with the disarticulation of the racemes of spikelets into units (Figure 1) consisting of the internode of the rachis of the raceme, one spikelet (bearing one fruit), and a pedicel bearing a second spikelet, which is either vestigial or stami-

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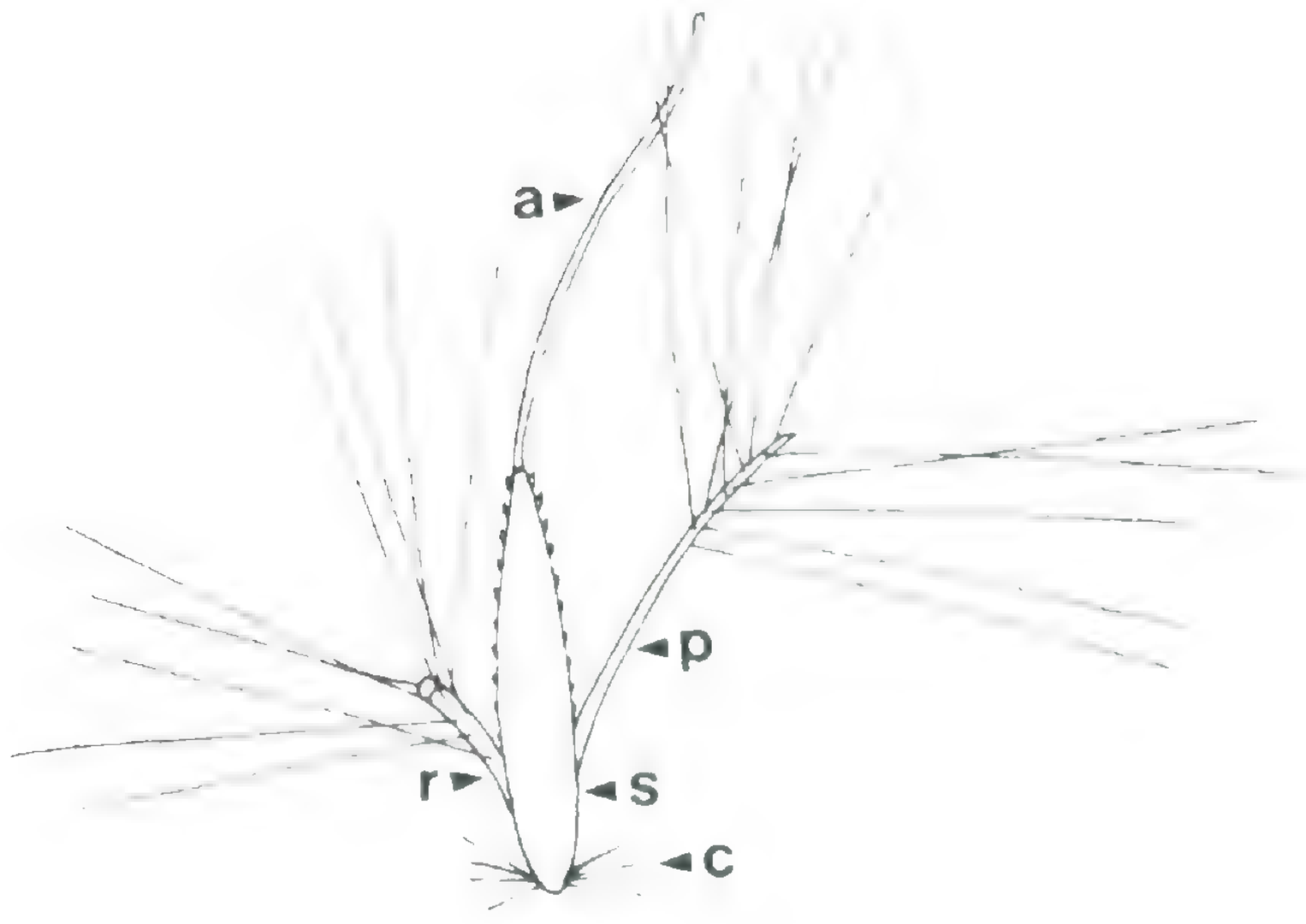

Figure 1. **Diaspore of Andropogon glomeratus var. pumilus,** many hairs of callus, pedicel and rachis internode omitted. a – awn (only base shown), c – callus hairs, p – pedicel (pedicelled spikelet completely suppressed), r – rachis internode, s – spikelet (showing lower glume with marginal prickle hairs).

nate and caducous. The spikelet itself is glabrous except for short (less than 5 mm) hairs on the callus, but the rachis internode and pedicel of many species bear long hairs (1–13 mm, especially toward the apex). These hairs, as well as the rachis internode and pedicel spread horizontally at maturity and, when the atmosphere is dry, form a plume. This unit of dispersal, or diaspore, is then ready to be carried away by the wind. The dispersal distance of plumed diaspores increases as height of release of the diaspores, wind velocity, and convection (vertical air movement) increase. Dispersal decreases as terminal or fall velocity of the diaspore, density and height of surrounding vegetation, and atmospheric humidity and precipitation increase. Diaspores released from a higher point will take longer to fall to the ground and will be subjected to the atmospheric forces which may carry them about for a longer time. Doubling the height of release will double the dispersal distance in a constant wind and convection velocity (Sheldon & Burrows, 1973). The arrangement of the diaspores and hence their height of release is determined by the shape of the inflorescence. In *Andropogon virginicus* the spikelets are more or less evenly spaced over the upper

two-thirds of the plant. The spikelets of *A. bicornis* L. and *A. glomeratus* in contrast, are usually densely clustered toward the top of the stems. The average height of release of diaspores from the latter species is greater than from the former.

The terminal velocity of the diaspores of four species of *Andropogon* and two other species have been computed (Table 1). *Taraxacum officinale* Weber is included as a commonly known reference point. The value obtained here is close to the value (35.7 cm/sec) determined by Sheldon and Burrows (1973). Confidence in the biological importance of these mean values lies in their reproducibility (compare the values for two different plants of *Andropogon gyrans* obtained on different days) and apparent genetic base (compare the two populations of *A. longiberbis* Hackel). The terminal velocity of an object reflects its coefficient of aerodynamic drag. The lower the terminal velocity the greater is the force opposing the acceleration due to gravity. That the main source of the aerodynamic drag is the plume of Andropogon diaspores is shown by their performance after the hairy rachis internode and pedicel have been removed. The mean times required to fall through two m by the intact diaspores of *A. virginicus* and *A. longiberbis* (Gilchrist County population) are 6.1 and 5.4 seconds respectively. After the rachis internode and pedicel have been removed, the fall times are 1.0 and 1.2 seconds respectively. In these species there does not appear to be any strong relationship between terminal velocity and weight of the diaspores. The most important factors are the length and density of hairs on the rachis internode and pedicel.

The diaspore of *Schizachyrium scoparium* (Michx.) Nash (*Andropogon scoparius* Michx.) resembles that of Andropogons in structure. The shortness of the hairs on the rachis internode and pedicel (2–4 mm long) accounts for its relatively high terminal velocity (Table 1).

If the only movement of the air is constant and parallel to the ground at, for example, 150 cm/sec (5.4 km/hr), a diaspore of *Andropogon glomeratus* released from 100 cm above the ground will travel 750 cm away from the plant before reaching the ground (assuming the diaspore moves at the same velocity as the wind). If there is any convection, the rate of fall of the diaspore will be reduced and its potential dispersal distance increased. If the ratio of convection velocity to terminal velocity is greater than or equal to one, there will be no downward movement of the diaspore, and it

Table 1. Terminal velocity[a] ($\bar{x} \pm$ S.D.) and weight[b] of plumed diaspores of several species. (N = 30)

Taxon Collector, number State, County	Terminal velocity (cm/sec)	Weight (mg) mean
Andropogon virginicus *Campbell, 3782* Florida, Jackson	32.3 ± 4.6	0.35
A. glomeratus var. *pumilus* Vasey *Campbell, 3739* Florida, Lee	20.1 ± 1.8	0.32
A. gyrans plant I *Campbell, 3872* plant II Florida, Jackson	26.9 ± 2.7 29.8 ± 3.3	—— 0.75
A. longiberbis *Campbell, 3910* Florida, Gilchrist	37.8 ± 4.5	0.65
A. longiberbis *Campbell, 3734* Florida, Dade	41.3 ± 6	——
Schizachyrium scoparium *V. L. Cory, 11,348* Texas, Galveston	101[c] ± 12	0.75–0.98[d]
Taraxacum officinale *Campbell* Massachusetts, Middlesex	31 ± 6.2	——

[a] In all cases except *Schizachyrium scoparium* (see note c) the measurements of terminal velocity where made by dropping the diaspores in still air from about 2 dm above a line two m above the floor. A stop watch was started as the diaspore passed through the two meter height and stopped when it reached the floor. It appeared that all these diaspores reached terminal velocity rapidly, before reaching the two meter line. Sheldon and Burrows (1973) showed that plumed diaspores of the Compositae with terminal velocities of the same range as these reached terminal velocity quickly.

[b] Mean weight was determined by weighing 20 diaspores together and dividing the total by 20.

[c] Terminal velocity determined by dropping diaspores from two and one m separately and constructing a graph of height of release against time of fall. The slope of the line of the two data points is the terminal velocity (Sheldon & Burrows, 1973). The value given here is near that recorded for the same species (91 cm/sec) by Rabinowitz & Rapp (1981).

[d] From Roos and Quinn, 1977.

could be dispersed an infinite distance on the slightest breeze (Burrows, 1973).

In the Compositae, the pappus, which forms the plume, is sensitive to humidity (Sheldon & Burrows, 1973). At high humidities the pappus closes and is thereby protected from damage by raindrops and less likely to be released from the plant when raindrops could increase the downward movement of the diaspores. *Andropogon* diaspores are also hygroscopic. Diaspores of *Andropogon gyrans* suspended over water in a closed container radically change their configuration. The rachis internode, pedicel, and their many hairs quickly become tightly appressed to the spikelet. Although their terminal velocity was not determined in this condition, it is assumed that it would be about the same as a spikelet without rachis internode and pedicel. When these diaspores were placed under a lamp, the rachis internode, pedicel, and hairs spread to their horizontal position in a few seconds.

There are two aspects to the dispersal of a colonizing group. First, rapid spread in a local area which is edaphically and otherwise appropriate is the *sine qua non* of colonization. Observations of *Andropogon* dispersal in the eastern United States clearly indicate that the density of diaspores falls rapidly away from the plant. Dispersal appears to follow the pattern of *Senecio jacobaea* (Compositae) in which 60% of the plumed diaspores fell at the base of the plant, only 0.39% travelled beyond 4.6 m from the edge of the plants, 0.08% beyond 9 m, 0.02% beyond 18 m, and 0.005% greater than 36 m from the plot containing the plants (Harper, 1977).

Some habitats, like roadsides, may be more or less continuous, but most sites colonized by Andropogons, like fields, are discontinuous. Hence the second aspect of dispersal in connection with colonization is the transport of diaspores away from one locality to another suitable one some distance away. As Harper (1977) points out, "successional species are doomed in their present habitats, and their continued survival depends on escape and establishment elsewhere." The general process of colonization, then, is like that of Composites with specialized mechanisms for wind dispersal in which there are "isolated individuals over a great distance which may subsequently act as foci for new infections".

Under normal atmospheric conditions dispersal of diaspores away from the population to a distant and suitable new site may be a rather unlikely event. Long-distance dispersal becomes a greater

likelihood in extreme weather conditions such as hurricanes, tropical storms, and thunderstorms. From 1885 to 1971 inclusive, 160 tropical storms entered or significantly affected Florida (Anon, 1974). A little over half of these were of hurricane intensity (winds greater than 74 mph). The frequency of occurrence of hurricane force winds in any given year varies considerably: one in six around Miami, one in twenty-five in Tampa, one in eight in Tallahassee, and one in one hundred in Jacksonville, the least affected region in the state (Anon, 1974). Florida is the most strongly hit state in the southern United States. The usual hurricane tracks after passing through Florida — either to the northeast along the Atlantic Coastal Plain, or to the west into the Gulf of Mexico (Gentry, 1974) —pass over the center of greatest diversity of species of *Andropogon* in the United States and the area of their greatest prominence in the overall flora.

The tropical storm season of eastern North America overlaps with the period of diaspore dissemination in *Andropogon*. The average frequency of tropical cyclones (winds 39–73 mph) and hurricane peaks from August to October (Dunn & Miller, 1960). There is an average of 1.5, 2.6, and 1.9 tropical storms in each of these months respectively and 0.9, 1.6, and 0.8 hurricanes per month in the North Atlantic region in these three months respectively. *Andropogon* diaspores mature in late August, September, and especially October and November. As pointed out earlier, the dispersal capacity of the diaspores falls markedly when humidity is high. So the diaspores must be picked up by winds which are relatively dry (or very powerful). Once the diaspore is inside a storm itself, it is likely to be carried for a great distance.

Thunderstorms, though less powerful and more local, occur frequently enough to be potentially important modes of dispersal for *Andropogon* diaspores.

There is no direct evidence of the extent to which these diaspores are transported by storms. However, there is one possible example of long-distance dispersal. *Andropogon bicornis* is a common species of South and Central America and the West Indies. It has never been reported for the United States, and I have never seen it in my field work in South Florida. There is one specimen of this plant collected by F. C. Craighead in northern Monroe County in October of 1962 (deposited in the herbarium of the Fairchild Tropical Garden in Miami, Florida). It was identified as *A. floridanus*

Scribner, but the lack of awns and the conspicuous, staminate pedicelled spikelets leave no question of its being *A. bicornis*. It is possible that it was transported from the West Indies during Hurricane Donna in 1960. This was the most powerful hurricane in Florida's history, and its track passed within 30 miles of the site where Craighead found the plant. The nearest known localities of *A. bicornis* are in Cuba, over 300 km from Craighead's collecting site. Long-distance wind dispersal is also suspected in another genus of the Andropogoneae, *Bothriochloa* Kuntze, in which 15 of the 18 New World Species show major disjunctions between North and South America (Allred, 1981). After the diaspore becomes established following long-distance dispersal it must reproduce itself if the new site is to be colonized. The capacity for apomictic seed production has not been reported for *Andropogon* sensu stricto (Connor, 1979; Campbell, 1983). Most North American Andropogons are cespitose, so colonization depends upon sexual seed production. If these plants were self-incompatible, a second genotype would have to be present within the range of pollen dispersal for fertilization and seed production to be effected. The probability of two plants of differing genotypes arriving at the same place within one life span is much less than that of the establishment of a single individual. The fact that most North American Andropogons (and certainly the most vigorous colonizing species) are self-compatible and frequently cleistogamous (Campbell, 1982) increases the likelihood of the effectiveness of long-distance dispersal (Baker, 1953).

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LITERATURE CITED

Allred, K. 1981. Cousins to the South: Amphitropical disjunctions in *Bothriochloa* (Graminae). Abstract from Bot. Soc. Amer. meetings, Bloomington, Indiana.

Anon. 1979. Climates of the States. 2 vols. Officials of the National Oceanic and Atmospheric Administration, U.S. Dept. of Commerce. Water Information Center, Inc. New York.

BAKER, H. G. 1953. Race formation and reproductive effort in flowering plants. Symp. Soc. Exptl. Biol. 7: 114–143.

BAZZAZ, F. A. 1975. Plant species diversity in old-field successional ecosystems in Southern Illinois. Ecology **56:** 485–488.

BURROWS, F. M. 1973. Calculation of the primary trajectories of plumed seeds in steady winds with variable convection. New Phytol. **72:** 647–664.

CAMPBELL, C. S. 1982. Cleistogamy in *Andropogon* (Gramineae). Amer. J. Bot. **69:**1649–1658.

———. 1983. Systematics of the *Andropogon virginicus* complex (Gramineae). J. Arn. Arb. (In press).

CONNOR, H. E. 1979. Breeding systems in grasses: a survey. New Zealand J. Bot. **17:** 547–574.

DUNN, G. E., & B. I. MILLER. 1960. Atlantic hurricanes. Louisiana State University Press. 326 pp.

GENTRY, R. C. 1974. Hurricanes in South Florida. p. 73–81 *In:* Gleason, P. J. (ed.). Environments of South Florida: past and present. Memoir **2,** Miami Geological Society. 452 pp.

GOLLEY, F. B. 1965. Structure and function of an old-field broomsedge community. Ecol. Monogr. **35:** 113–137.

HARPER, J. L. 1977. Population biology of plants. Academic Press. London. 892 pp.

KEEVER, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monogr. **20:** 229–250.

RABINOWITZ, D., & J. K. RAPP. 1981. Dispersal abilities of seven sparse and common grasses from a Missouri prairie. Amer. J. Bot. **68:** 616–624.

ROOS, F. J., & J. A. QUINN. 1977. Phenology and reproductive allocation in *Andropogon scoparius* (Gramineae) populations in communities of different successional stages. Amer. J. Bot. **64:** 535–540.

SHELDON, J. C., & F. M. BURROWS. 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytol. **72:** 665–675.

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ON THE TAXONOMIC STATUS OF *LOPHIOLA AUREA* KER-GAWLER

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Familial and tribal treatments of the Haemodoraceae have been inconsistent, and there has been disagreement among various authorities over the inclusion of *Lophiola aurea* in the family (Geerinck, 1969).

Lophiola aurea = (*L. americana* (Pursh) Wood; see Robertson, 1976), which is the only species of *Lophiola,* grows in acid, pine-barren bogs from New Jersey to Florida, with a disjunct Nova Scotian population. The species has been variously treated, and placed in the tribe Conostyleae of the Amaryllidaceae (Pax, 1930), in the tribe Haemodoreae (Geerinck, 1969), and the Conostyleae of the Haemodoraceae (Hutchinson, 1973). Ornduff (1979), basing his conclusion on gross morphology and chromosome numbers, suggested that *L. aurea* is more closely allied with the tribe Haemodoreae and possibly with the genus *Lachnanthes,* the only other North American member of the Haemodoreae. However, Robertson (1976) investigated vegetative morphology, Simpson and Dickison (1981) investigated anatomy, and Simpson (1981) embryology, of *Lachnanthes* and *Lophiola,* and they found few similarities between these taxa. Our phytochemical and palynological studies of various taxa of the Haemodoraceae further suggest that *Lophiola aurea* is not closely related to other genera of Hutchinson's Haemodoreaceae.

MATERIALS AND METHODS

Pollen from living and dried herbarium material was used in this study. Live pollen was prepared for transmission electron microscopy (TEM) by fixation in cacodylate-buffered gluteraldehyde-formaldehyde followed by fixation with osmium tetroxide, dehydration in an ethanol series, and embedding in Dow Epoxy Resin-334 (DER-334). Pollen removed from herbarium specimens was acetolyzed and prepared for TEM by dehydration in an ethanol series, and embedded in DER-334. Sectioning was done on an LKB-I ultramicrotome; the sections were post-stained in uranyl acetate-lead citrate,

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and viewed on a Philips EM-300. Pollen was prepared for scanning electron microscopy (SEM) by mounting the pollen on stubs with the high vacuum wax Apiezon W-100, coated with gold-palladium, and viewed on a Coates and Welter Field Emission Electron Microscope.

Dried, defatted, above ground parts of *Lophiola aurea* (Edwards, *s.n.*, New Jersey, CONN) were extracted with 95% ethanol. Thin-layer chromatography of the extract (Silica gel, ethyl acetate-benzene, 1:2) indicated the presence of two phenolic compounds (positive color reaction with diazotized *p*-nitroaniline) having R_f s 0.3 and 0.1. Column chromatography of the mixture over silica gel with ethyl acetate and increasing amounts of ethanol (95%) resulted in the isolation of the less polar compound as a pale yellow solid of mp 219–223° (ethyl acetate-petrol ether).

RESULTS

Palynology

Hutchinson (1973) includes ten genera in the tribe Haemodoreae. Three genera and three species were investigated palynologically; *Lachnanthes caroliana* (Lam.) Dandy, (*Weatherley s.n.*, Connecticut, CONN); *Wachendorfia paniculata* Burm., (*Zavada 501*, Cult., CONN); and *Xiphidium caeruleum* Aubl., (*Wolfe 234*, Surinam, CONN). Pollen of this tribe is monosulcate (Erdtman, 1952; Radulescu, 1973; present study). Pollen of *Lachnanthes caroliana* averages 36–44 μm along its long axis and sculpturing is scabrate to verrucate (fig. 1). Wall structure is atectate and infrequently traversed by minute channels (fig. 2). No endexine is evident. Pollen of *Wachendorfia paniculata* averages 55–58 μm along its long axis and sculpturing on the proximal and distal faces of the pollen grain is scabrate to pustulate (fig. 5). Separating the proximal and distal faces of the pollen grain is a psilate ridge (figs. 4, 5). Wall structure on the proximal and distal faces is granular with large and small spherical to irregularly shaped granules closely appressed to one another (fig. 3; cf. "structure grenue" of Van Campo and Lugardon, 1973). The wall structure of the psilate ridge differs in having a thick tectum with a granular layer beneath (fig. 4). No foot layer or endexine is evident. Pollen of *Xiphidium caeruleum* averages 40–55 μm along its long axis and pollen grains are psilate (figs. 6, 7). Wall structure is tectate with the tectum fused to irregularly shaped rod-like structures which are often interspersed with granules (fig. 7).

The tectum is occasionally traversed by minute channels (fig. 7). No foot layer or endexine is evident.

Hutchinson (1973) includes six genera in the tribe Conostyleae. Three genera and three species were investigated palynologically; *Anigozanthos flavus* D.C. ex Red., (*Edwards s.n.*, "1977", CONN); *Conostylis setosa* Lindl., (*Wolfe s.n.*, Australia, CONN); and *Lophiola aurea* Ker-Gawler, (*Edwards s.n.*, New Jersey, CONN). Pollen of this tribe is 2–8-porate, except *Lophiola aurea* which is monosulcate (Erdtman, 1952; Radulescu, 1973; present study). Pollen of *Anigozanthos flavus* averages 36–44 μm along its long axis and is diporate with the pores located opposite one another along its long axis (fig. 8). Sculpturing is roughly scabrate and wall structure is atectate (figs. 8, 9). No endexine is present. Pollen of *Conostylis setosa* is triporate averaging 22–29 μm along its long axis and pollen wall sculpturing is roughly scabrate (fig. 10). Wall structure is atectate and no endexine is present (fig. 11). Pollen of *Lophiola aurea* is monosulcate averaging 29 μm along its long axis. Pollen grains are finely reticulate (fig. 13). Wall structure is tectate-columellate with a thin foot layer and no endexine (fig. 12).

Phytochemistry

The yellow-colored compound isolated from silica gel chromatography had λmax (EtOH) 227 (Logϵ 4.49), 293 (4.51), and 330 sh (3.90) nm. $\sqrt{}$max 3270, 1650, and 1520 cm.$^{-1}$ δ (persilyl ether in $CDCl_3$ 60MHz) 7.22 (2H, d, 9Hz), 7.12 (2H, d, 9Hz), 6.76 (2H, d, 9Hz), 6.61 (2H, d, 9Hz), 5.94 (2H, dd, 2.5Hz), 5.76 (1H, s), 5.66 (1H, d, 2Hz), 5.22 (1H, q, 12 and 5Hz), 4.36 (1H, d, 12Hz), 3.00–2.78 (2H, m). M^+ (%) 542 (.02); 416.885, $C_{24}H_{16}O_7$ (65); 296.0317, $C_{16}H_8O_6$ (52); 270.0520, $C_{15}H_{10}O_5$ (3); 126 (40) and 94 (100). The MS of the persilyl ether had M^+ 974 indicating the presence of six hydroxyl groups in the molecule. Comparison of these spectral data with those published for the biflavanone GB–1a (Jackson et al., 1967 and Bandaranayake et al. 1975) indicated that the compound was 5, 7, 4′, 5″, 4‴ -hexahydroxy [3,8″] biflavanone.

DISCUSSION

The pollen data underscore the unique status of *Lophiola aurea* in the Haemodoraceae. *Lophiola aurea* is the only species investigated exhibiting the tectate-columellate wall structure and reticulate exine

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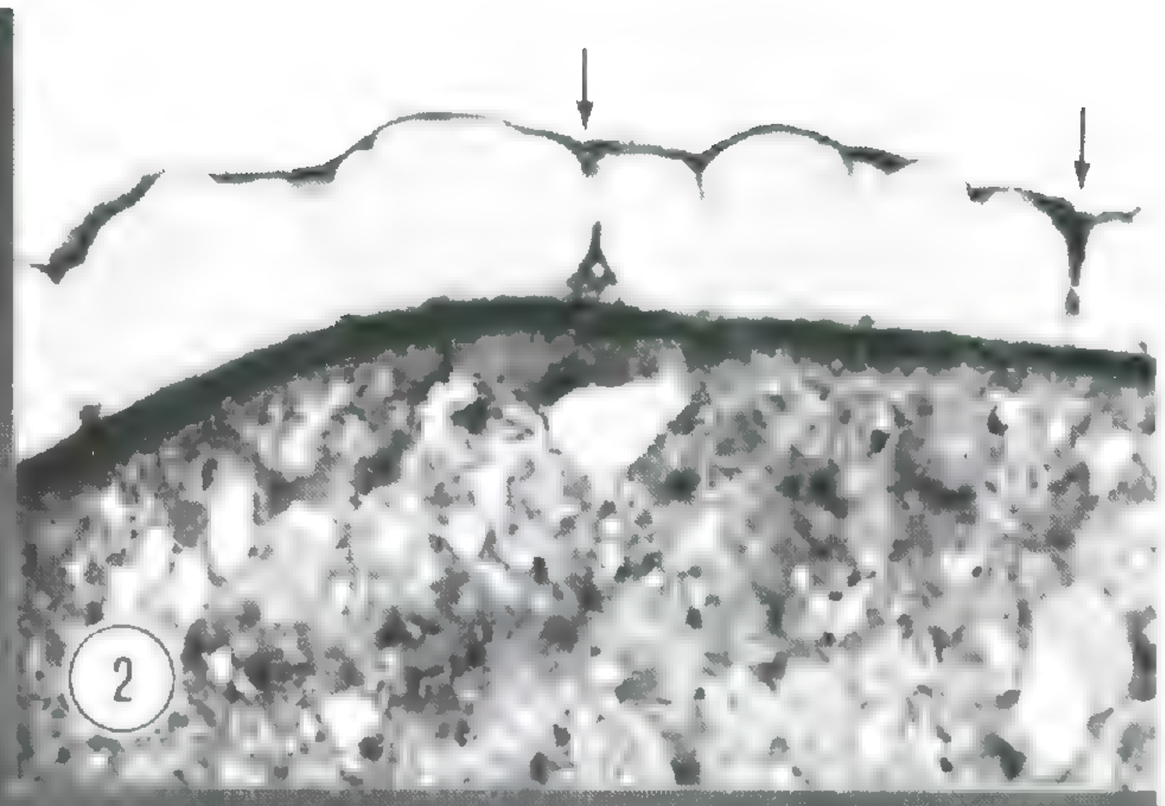
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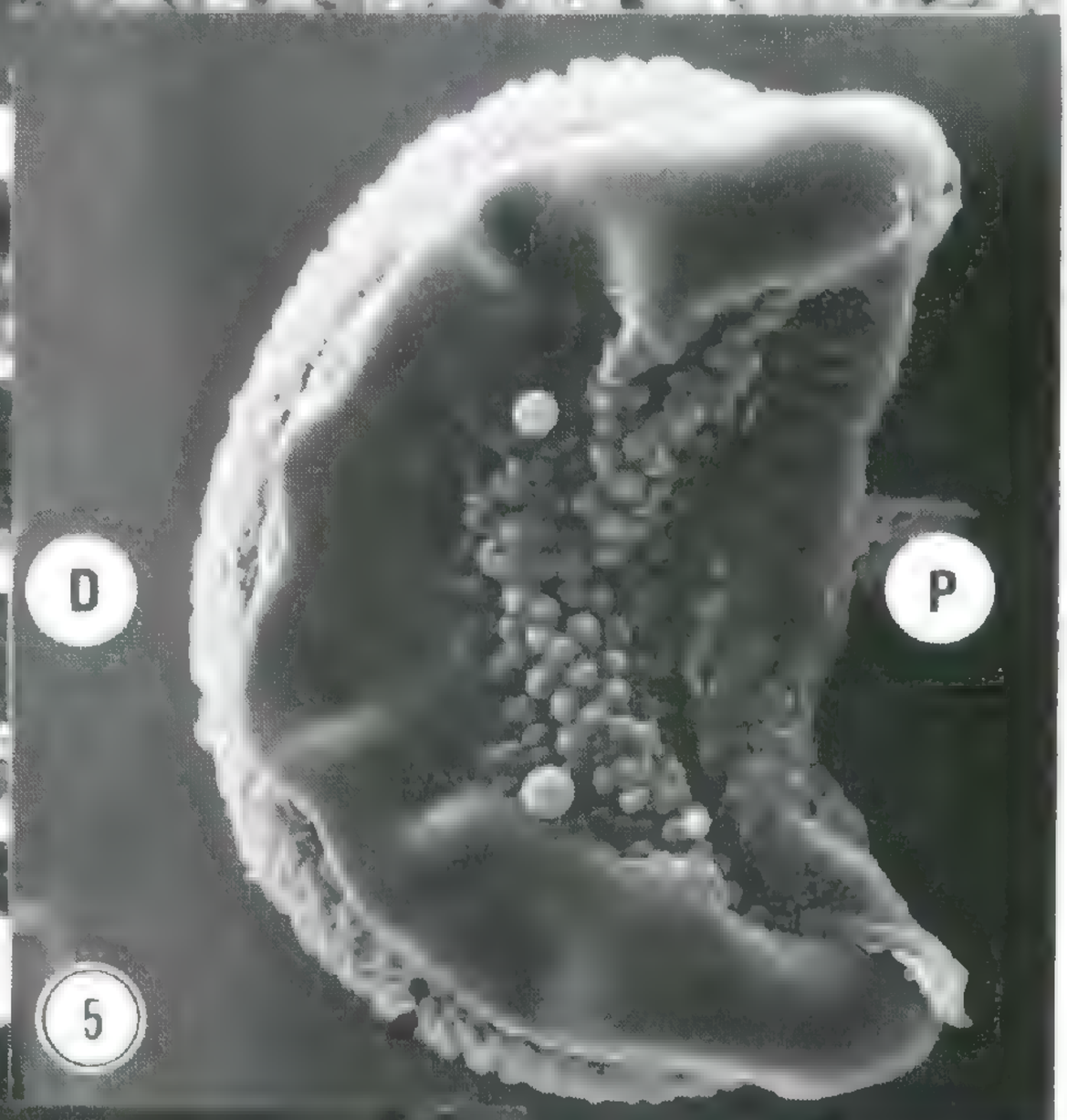
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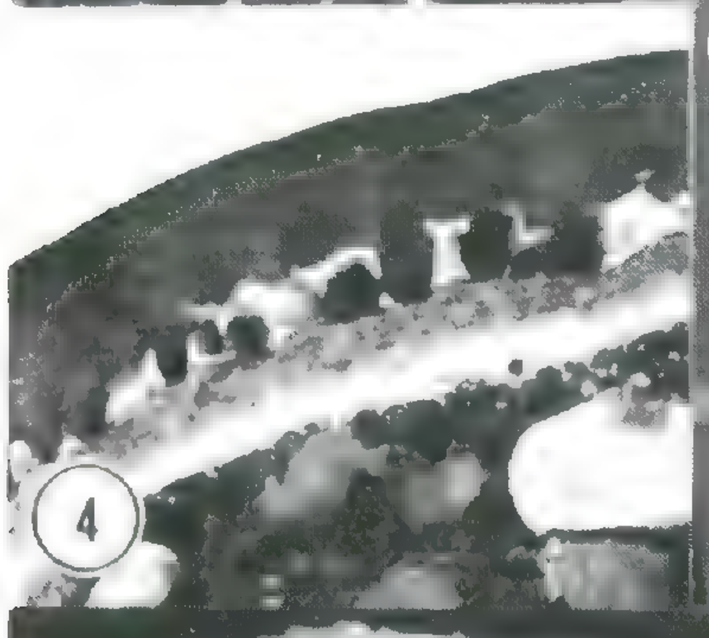
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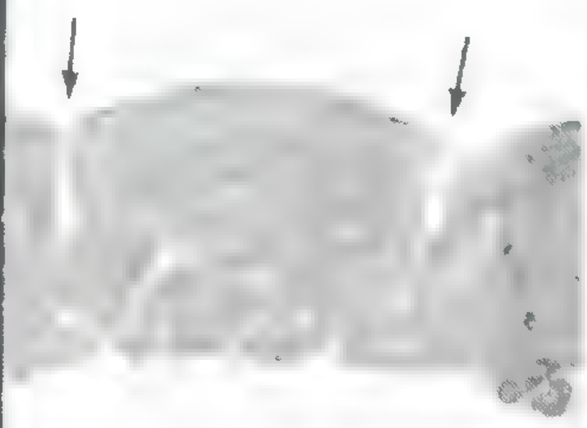
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sculpturing. The five other genera investigated have atectate or tectate-granular wall structure. The monotypic species *Lanaria plumosa* Ait., placed in the Haemodoraceae by Hutchinson (1973), is the only other genus reported to have reticulate exine sculpturing (Erdtman, 1952). The reticulate exine pattern is usually accompanied by the tectate-columellate wall structure. Thus, *Lophiola* and *Lanaria* are the only genera of the Haemodoraceae, as assigned by Hutchinson, exhibiting palynological features not found among the other genera of the family (Erdtman, 1952; present study). Their palynological features are more similar to those of some members of the closely related family Tecophilaeaceae (sensu Hutchinson). However, data on vegetative morphology (Robertson, 1976), anatomy (Simpson and Dickison, 1981), embryology (Simpson, 1981), and palynology and chemistry (present study) more firmly establish the differences between *L. aurea* and other members of the Haemodoraceae than the taxonomic affinities of *L. aurea*. This is due to the paucity of detailed morphological, anatomical, palynological and chemical data on the Tecophilaeaceae and other closely related families to the Haemodoraceae. Placement of *L. aurea* in any of these families would make that designation as tenuous as its present status.

Excluding *Lophiola aurea* (and *Lanaria plumosa*) from the Haemodoraceae highlights the stenopalynous nature of the remaining genera in each tribe. This lends support to a treatment of the Haemodoraceae similar to Hutchinson's, save the inclusion of *Lophiola* and *Lanaria*. The tribe Haemodoreae then only includes taxa with monosulcate pollen, a more primitive situation than the 2–8-porate

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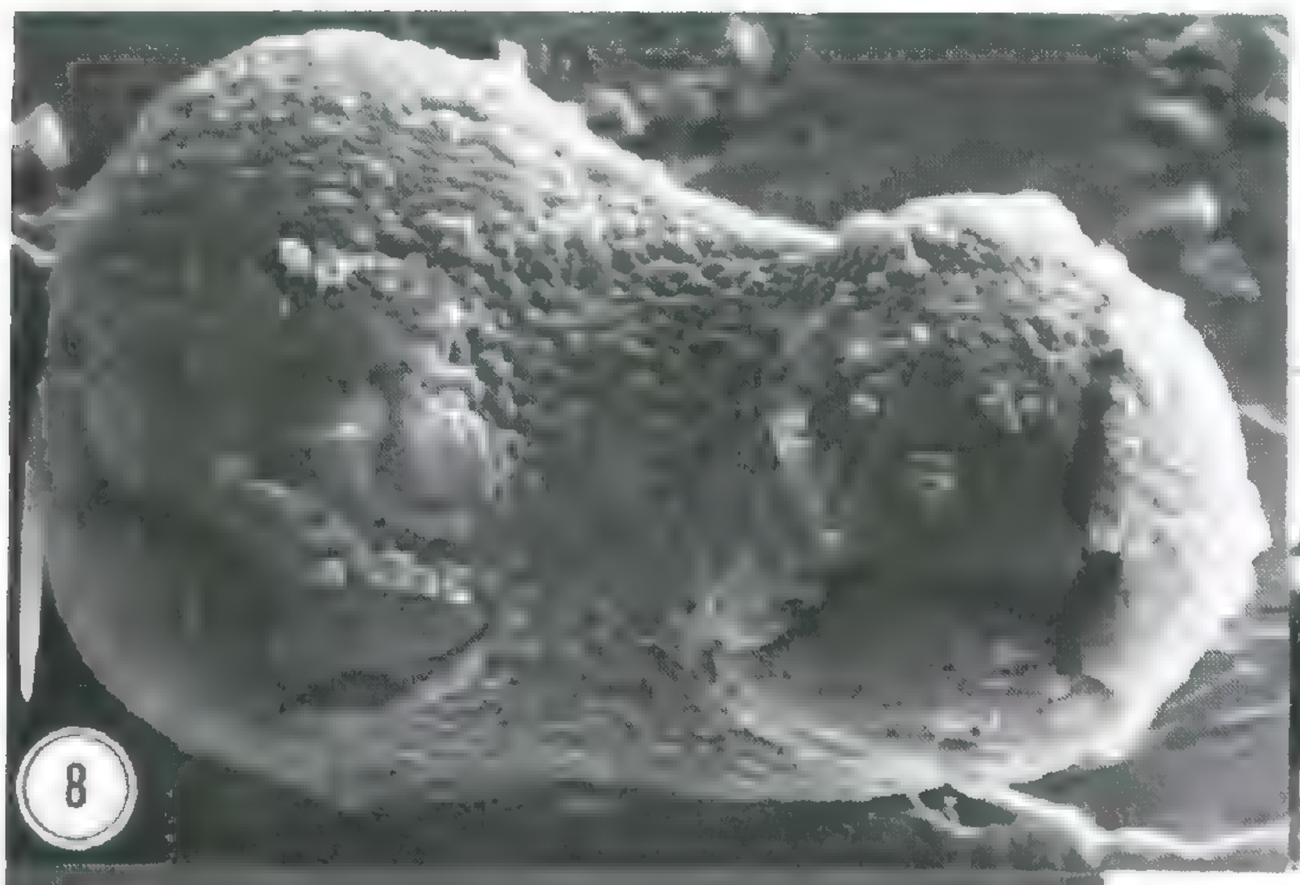
Figures 1–7. **Pollen of the Haemodoreae.** Figure **1.** *Lachnanthes caroliana*, acetolyzed, SEM × 1,530. Figure **2.** *L. caroliana*, unacetolyzed, TEM showing atectate wall structure, minute channels (arrows), and thin intine, × 17,000. Figure **3.** *Wachendorfia paniculata*, unacetolyzed, TEM showing spherical to irregularly shaped granules comprising the wall of the distal face of the pollen grain, note thin intine, ×14,200. Figure **4.** *W. paniculata*, unacetolyzed, TEM showing wall structure in the region of the psilate ridge, note thick tectum and granular layer beneath resting on a thin intine, ×14,200. Figure **5.** *W. paniculata*, acetolyzed, SEM showing scabrate and pustulate exine sculpturing on the proximal (P) and distal (D) faces of the pollen grain, note psilate ridge separating these regions, × 2,850. Figure **6.** *Xiphidium caeruleum*, acetolyzed, SEM showing sulcus, × 2,850. Figure **7.** *X. caeruleum*, acetolyzed, TEM showing granular infrastructure, also with irregularly shaped rods, note the minute channels (arrows) traversing the relatively thick tectum, ×25,000.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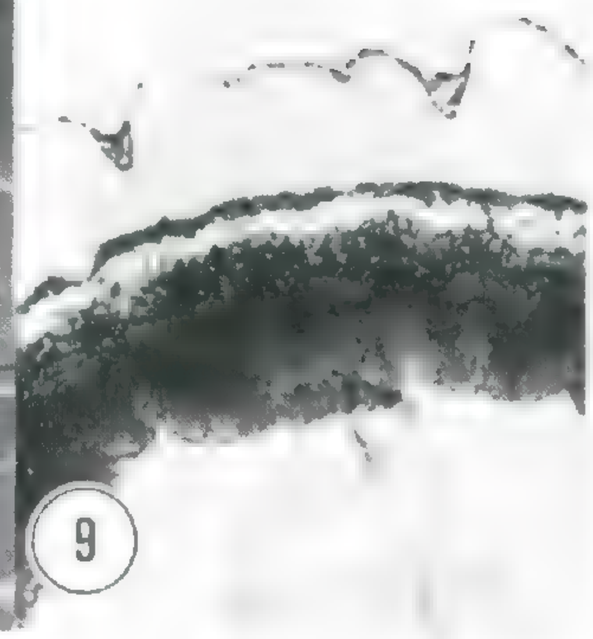
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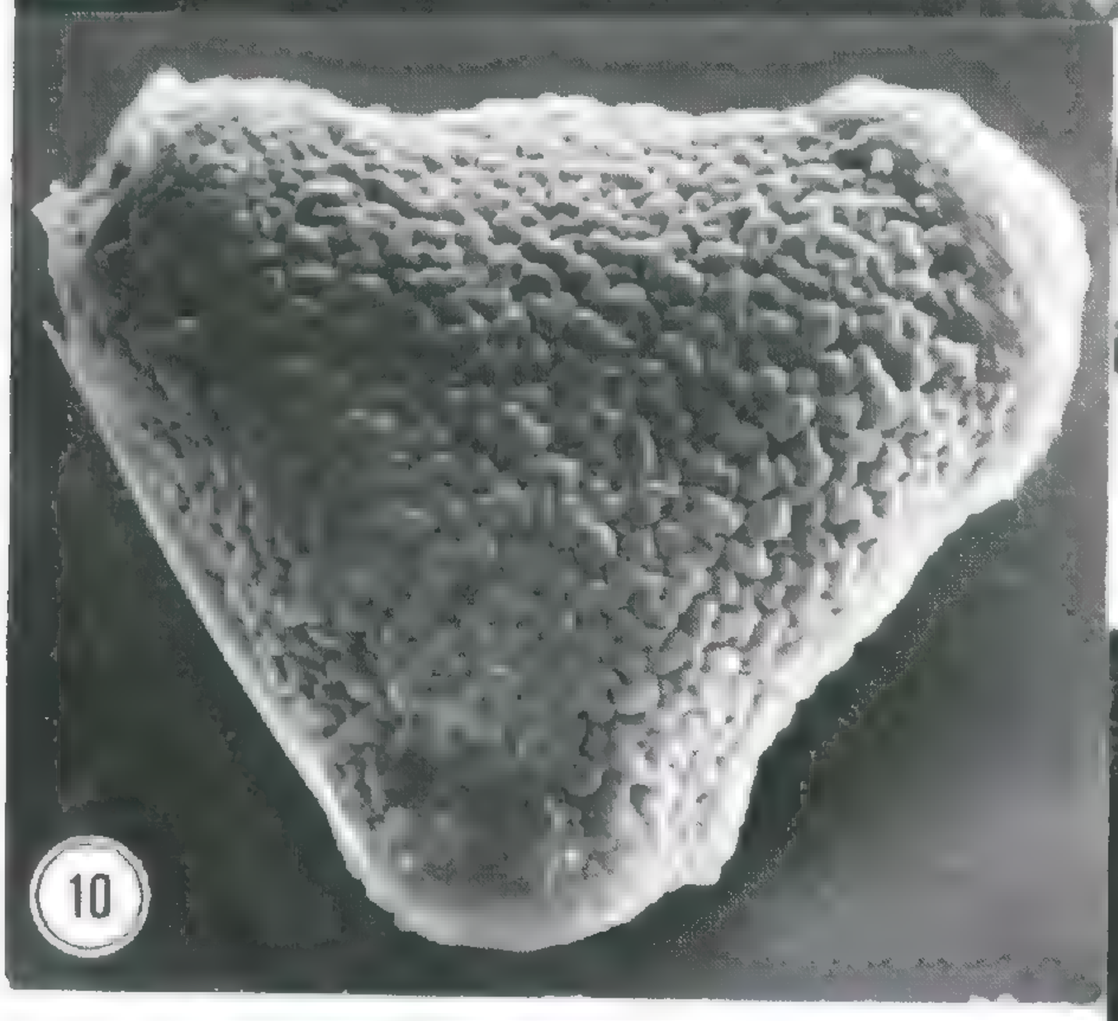
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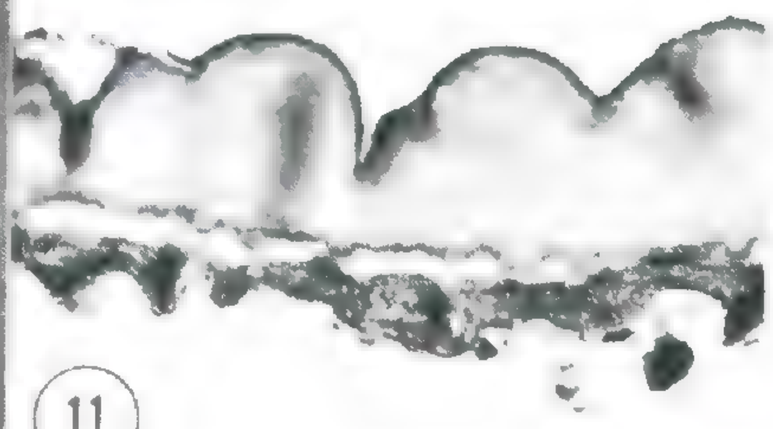
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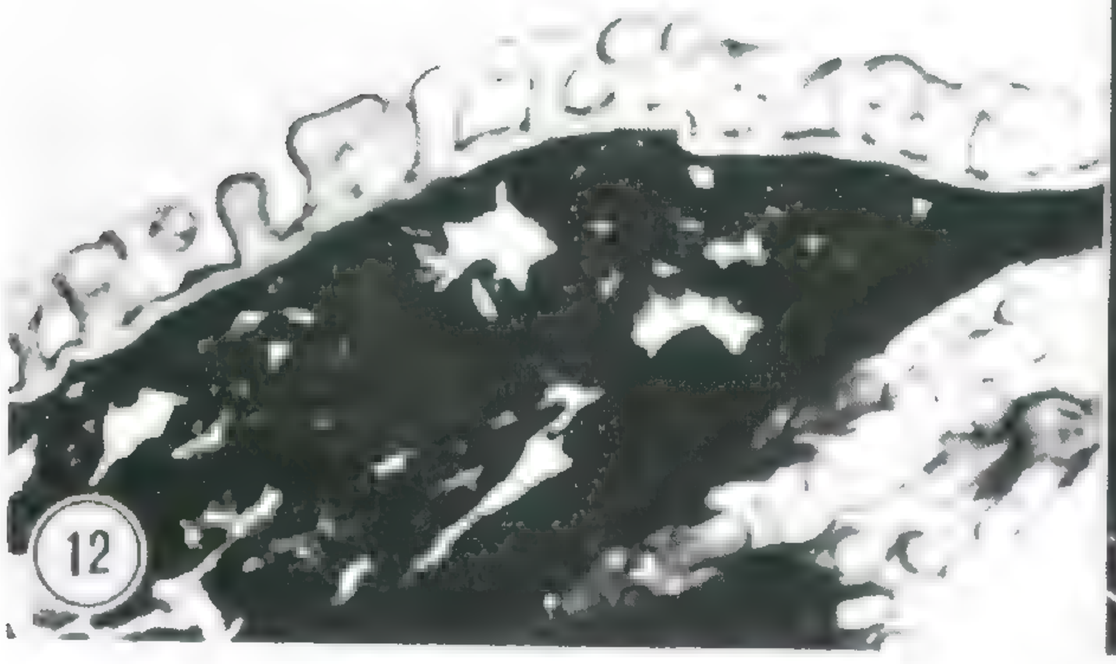
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pollen characteristic of the tribe Conostyleae. The evolutionarily advanced status of the entire family is supported by the occurrence of the atectate and granular wall structure: wall structural types occurring in the more advanced taxa of other monocot orders (Walker & Doyle, 1975; Zavada, manuscript in preparation).

Investigations of the yellow, orange, brown, and purple pigments present in the colorful root systems, flowers, and seed capsules of eight genera of the Haemodoraceae *(Anigozanthos, Conostylis, Haemodorum, Lachnanthes, Macropidia, Phlebocarya, Wachendorfia,* and *Xiphidium)* have shown them to be derivatives of either 9-phenalenone or naphthoxanthenone. Furthermore, secondary metabolites containing the phenalenone nucleus, or having structures which can reasonably be presumed to have been derived from an intact phenalenone, are rare in nature; their occurrence seems to be restricted to four genera of hyphomycetes (Fungi Imperfecti), one genus within the class Discomycetes, and one family of higher plants. These chemical compounds seem to be chemotaxonomic markers for the Haemodoraceae (Cooke & Edwards, 1981).

Lophiola aurea lacks obvious pigmentation except for its pale yellow flowers, and previous investigation of the plant (Edwards, et al., 1970) has shown it to be devoid of phenalenone and related pigments. The present study, while confirming the absence of phenalenones, has identified the biflavanoid 5, 7, 4′, 5″, 7″, 4‴-hexahydroxy [3,8″] biflavanone (GB 1a) in extracts of *L. aurea,* a compound which has been isolated previously from species of *Garcinia* (Guttiferae) (Jackson, et al., 1967; Bandaranayake, et al., 1975). Biflavonoid compounds have been isolated from some 20 plant families, none of which is monocotyledonous (Geiger & Quinn, 1975); furthermore, no flavonoids have been isolated from the Haemodoraceae. There is an account of the chromatographic

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Figures 8–13, **Pollen of the Conostyleae.** Figure **8.** *Anigozanthos flavus,* acetolyzed, SEM showing the two opposing pores, ×1,760. Figure **9.** *A. flavus,* unacetolyzed, TEM showing atectate wall structure and thick intine, × 17,100. Figure **10.** *Conostylis setosa,* acetolyzed, SEM showing triporate condition, × 2,370. Figure **11.** *C. setosa,* unacetolyzed, TEM showing atectate wall structure and thin intine, × 20,100. Figure **12.** *Lophiola aurea,* unacetolyzed, TEM showing tectate-columellate wall structure, × 20,100. Figure **13.** *L. aurea,* acetolyzed, SEM showing reticulate exine sculpturing on the distal face of the pollen grain, a sculpturing type found in the monotypic genus *Lanaria plumosa* of the Haemodoraceae, × 4,220.

identification of flavonoids in a *Haemodorum* sp. (Bate-Smith, 1968; Gornall, et al., 1979), but no flavonoids have been isolated; the phenalenone pigments are so abundant in *Haemodorum* that the identification of flavonoids by chromatographic methods alone must be regarded as tentative at best.

We feel that the chemical findings reported here: absence of phenalenone and naphthoxanthenone pigments and the presence of a biflavonoid, in conjunction with the palynological data, provide good chemotaxonomic and palynological evidence against the inclusion of *Lophiola aurea* in the Haemodoraceae.

LITERATURE CITED

Bandaranayake, W. M., S. S. Selliah, M. U. S. Sultanbawa, & W. D. Ollis. 1975. Biflavonoids and xanthones of *Garcinia terpnophylla* & *G. echinocarpa*. Phytochemistry **14:** 1878–1880.

Bate-Smith, E. C. 1968. The phenolic constituents of plants and their taxonomic significance. J. Linn. Soc. (Bot.) **60:** 325–356.

Cooke, R. G., & J. M. Edwards. 1981. Naturally occurring phenalenones and related compounds. Fortschr. Chem. Org. Naturstöffe **40:** 158–190.

Edwards, J. M., J. A. Churchill, & U. Weiss. 1970. A chemical contribution to the taxonomic status of *Lophiola americana*. Phytochemistry **9:** 1563–1564.

Erdtman, G. 1952. *Pollen morphology and plant taxonomy. Angiosperms.* Chronica Botanica Co., Waltham, Mass.

Geerinck, D. 1968. Considerations taxonomique au sujet des Haemodoraceae et des Hypoxidaceae. (Monocotyledones). Bull. Soc. Roy. Bot. Belgique **101:** 265–278.

Geiger, H., & C. Quinn. 1975. Biflavonoids. *In:* "The Flavonoids," J. B. Harborne, T. J. Mabry, and H. Mabry, Eds., Academic Press, New York. pp. 692–742.

Gornall, R. J., B. A. Bohm, & R. Dahlgren. 1979. The distribution of flavonoids in the angiosperms. Bot. Not. **132:** 1–30.

Hutchinson, J. 1973. The families of flowering plants. 2nd Edition, Vol. II, Monocotyledons. Oxford Univer. Press, Oxford.

Jackson, B., H. D. Locksley, F. Scheinmann, & W. A. Wolstenholme. 1967. The isolation of a new series of biflavonones from the heartwood of *Garcinia buchananii* Baker. Tetrahedron Lett. 787–792.

Orndduff, R. 1979. Chromosome numbers and relationships of certain African and American genera of Haemodoraceae. Ann. Missouri Bot. Garden, **66:** 577–580.

Pax, F. 1930. Haemodoraceae. Nat. Pflanzenfam. ed. B. **15a:** 386–391.

Radulescu, D. 1973. La morphologie du pollen chez quelques Haemodoraceae. Lucrarile Gradinii Botanice Din Bucuresti, **1972-73,** pp. 123–132.

Robertson, K. R. 1976. The genera of Haemodoraceae in the southeastern United States. J. Arnold Arbor. **57:** 205–216.

SIMPSON, M. G. 1981. Embryological development of *Lachnanthes caroliniana* (Lam.) Dandy and *Lophiola aurea* Ker-Gawler (Haemodoraceae) and its taxonomic significance. Bot. Soc. America, Misc. Series, Pub. **160**, p. 78 (Abstract).

SIMPSON, M. G., & W. C. DICKISON. 1981. Comparative anatomy of *Lachnanthes* and *Lophiola* (Haemodoraceae). Flora **171:** 95–113.

VAN CAMPO, M., & B. LUGARDON. 1973. Structure grenue infratectale de l'ectexine des pollens de quelques gymnospermes et angiospermes. Pollen et Spores **15:** 171–197.

WALKER, J. W., & J. A. DOYLE. 1975. The basis of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Garden **62:** 664–723.

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THE FERN GENERA VITTARIA AND TRICHOMANES IN THE NORTHEASTERN UNITED STATES[1]

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Abstract. *Vittaria* is reported from 5 counties in Pennsylvania; *Trichomanes* from 24 counties in Connecticut, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, and Vermont. All are new state records except *Trichomanes* in Massachusetts. These ferns occur as gametophytes only, but in large conspicuous populations in crevices and grottos of moist, non-calcareous rock outcrops in canyon topography. The northernmost distribution of *Trichomanes* has not been established, but may parallel that of the oak-hickory forest type. *Vittaria* was not found north of the southern terminus of Pleistocene glaciation; its northern distribution may have been truncated by that event. *Vittaria* sites in northwestern Pennsylvania are well north of apparently suitable glaciated habitats in eastern Pennsylvania wnich house *Trichomanes* but not *Vittaria*.

Field botanists of the southern Appalachian Mountain and Plateau regions of the Eastern U.S. are familiar with the occurrence of conspicuous populations of fern gametophytes totally devoid of the sporophyte phase of the fern life cycle. Best known of these is the Appalachian *Vittaria* gametophyte which produces dense, vivid green colonies often dominating the flora of heavily shaded, moist outcroppings of non-calcareous rocks (Farrar, 1978). Less familiar but equally common are the filamentous gametophytes of the genus *Trichomanes* which form velvety cushions and tufts in the same habitats as *Vittaria* (Farrar, 1967; Wagner & Evers, 1963). Gametophytes of both genera have the ability to reproduce themselves vegetatively by means of gemmae and thus exist independently of and beyond the range of their sporophyte counterparts. Sporophytes of *Vittaria* are totally absent from Eastern U.S. uplands, and gametophytes of *Trichomanes* are known far north of the range of sporophytes of *Trichomanes petersii* and *Trichomanes boschianum* (with northernmost occurrences in Sevier Co., Tennessee and Hocking Co., Ohio respectively). It was, in fact, the recent discovery of *Trichomanes* gametophytes in Massachusetts (McAlpin & Farrar, 1978) that prompted this study.

[1]This study was supported by a grant from the National Geographic Society and made possible through a Faculty Improvement Leave from Iowa State University to the senior author.

In considering the origin of the Appalachian *Vittaria* gametophytes, Farrar (1978) proposed that they were possibly relicts of a Tertiary subtropical flora. In support of this hypothesis he cited the basic tropical affinity of the genus, the morphological and physiological differentiation of the Appalachian plants from all other known species of *Vittaria*, and the restriction of their occurrence to rock exposures predating and lying south of the borders of Pleistocene glaciation. It was also suggested that *Trichomanes* shared many of these characteristics and may have experienced a similar history.

The distribution of *Vittaria* and *Trichomanes* in the Northeastern U.S. has not been carefully studied previously. Since appropriate habitats here are abundant and continuous through the southern terminus of Pleistocene glaciation, this is an important area in which to investigate the factors limiting the distribution of these unusual plants and providing clues to their origin. They also constitute significant new additions to the floras of the northeastern states in which they occur.

METHODS

Field search for gametophytes of *Vittaria* and *Trichomanes* was conducted in portions of all states north of the Virginias, except Delaware and Rhode Island. Sites for investigation were identified through consultation with local field botanists and naturalists, analysis of physiographic maps, and checking of herbarium records of plants commonly associated with the gametophytes in more southern locations. Available time permitted investigation of only a fraction of the sites so identified. Herbarium vouchers were collected and prepared for deposit in the herbaria of Iowa State University, The New York Botanical Garden, and Millersville State College of Pennsylvania.

RESULTS AND DISCUSSION

Vittaria gametophytes were collected from 6 sites in 5 counties of Pennsylvania, and *Trichomanes* gametophytes were collected from 32 sites in 24 counties of Pennsylvania, Maryland, New Jersey, New York, Connecticut, Massachusetts, Vermont, and New Hampshire. These constitute new state records for all states listed except Massachusetts. A listing of collection sites and habitat substrates is given in Appendix 1.

Habitats of *Vittaria* and *Trichomanes* gametophytes in the Northeast are very similar to those in the Southeast: heavily shaded, moist outcroppings of non-calcareous rock. A significant difference is that occurrence of the gametophytes in the north seems to require development of these habitats on a larger scale. Gorges must be deeper and narrower, cliffs and waterfalls must be higher, and sites in general must offer greater buffering from climatic extremes than is required to support these plants in the south.

This extreme of habitat and microclimate specificity is well illustrated by the habitat of *Vittaria* at its northernmost station at Jake's Rocks in Warren County, Pennsylvania (Figure 1). This cave-like habitat was created by the cleavage and slumping of a huge sandstone block from an undercut cliff face. The massive, porous sandstone provides continuous moisture while moderating temperature through radiation and blockage of wind currents. Sufficient light (about 100 ft. c.) penetrates the "cave" opening to allow growth of *Vittaria*.

Trichomanes may also require wetter habitats in its northernmost localities. In the Catskill Mountains of New York and Green Mountains of Vermont it was collected only from crevices of rocks which were saturated with moisture, even during the relatively dry period

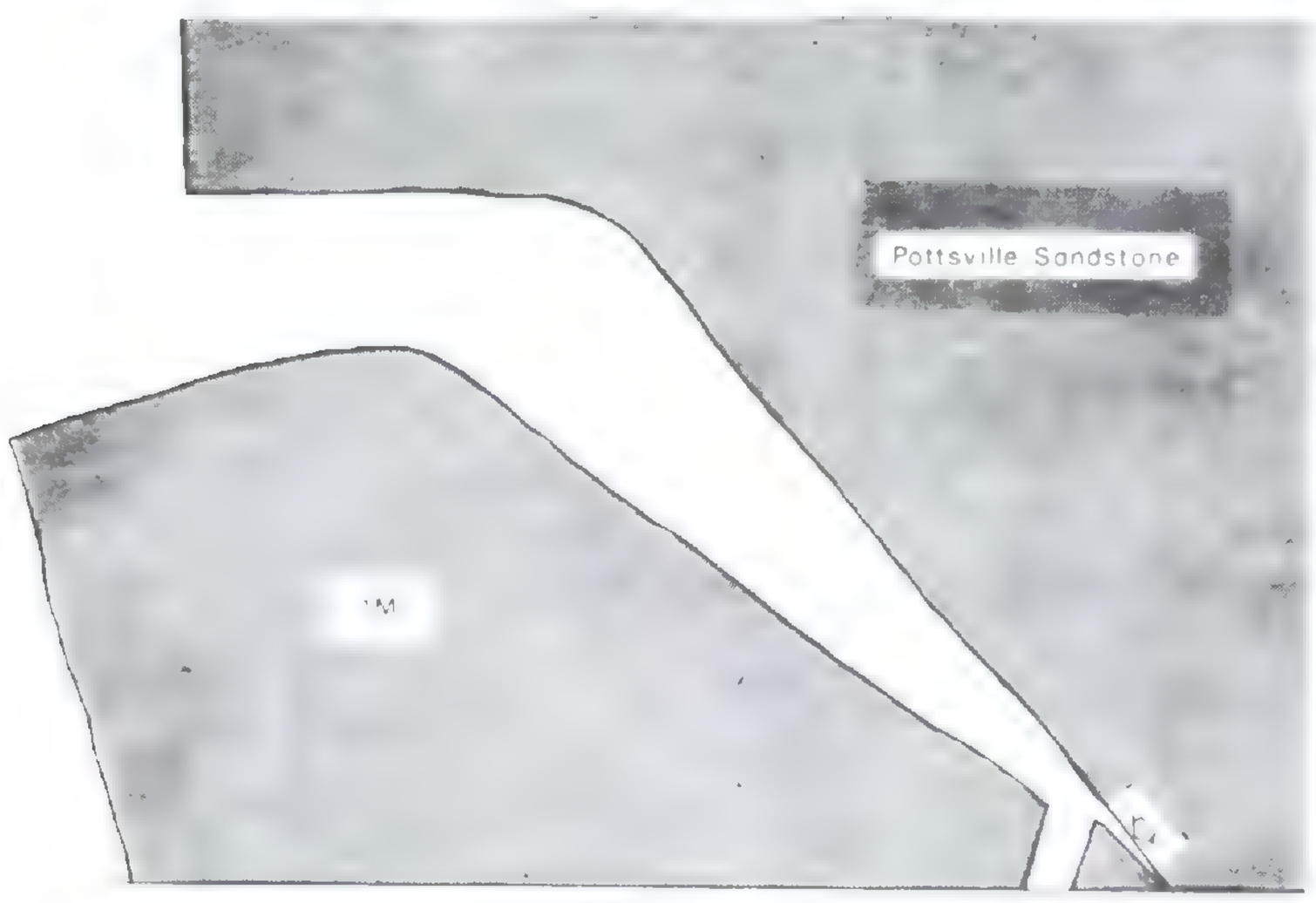

Figure 1. Diagrammatic cross section of the habitat of Appalachian *Vittaria* gametophytes at Jake's Rocks on the Allegheny Reservoir in Warren Co., Pennsylvania. Arrow indicates the microhabitat of *Vittaria*.

when collections were made. By contrast, in Pennsylvania and more southern areas, *Trichomanes* gametophytes often occur in habitats that are periodically quite dry.

The currently known distribution of *Vittaria* and *Trichomanes* in the Northeastern U.S. is presented in Figure 2. The distribution of *Trichomanes* clearly is not governed by the limits of glaciation. The northern limit of *Trichomanes* was not determined in this study as no sites north of the collections in New York and Vermont were investigated. A search for *Trichomanes* in habitats with suitable physical characteristics in the White Mountains of New Hampshire (Franconia Notch area) and Maine (Grafton Notch area) was unproductive. However, forest vegetation of these sites is decidedly more northern than the Central Hardwoods Oak-Hickory forest (Westveld, 1956; Little, 1971) typical of *Trichomanes* sites. On the

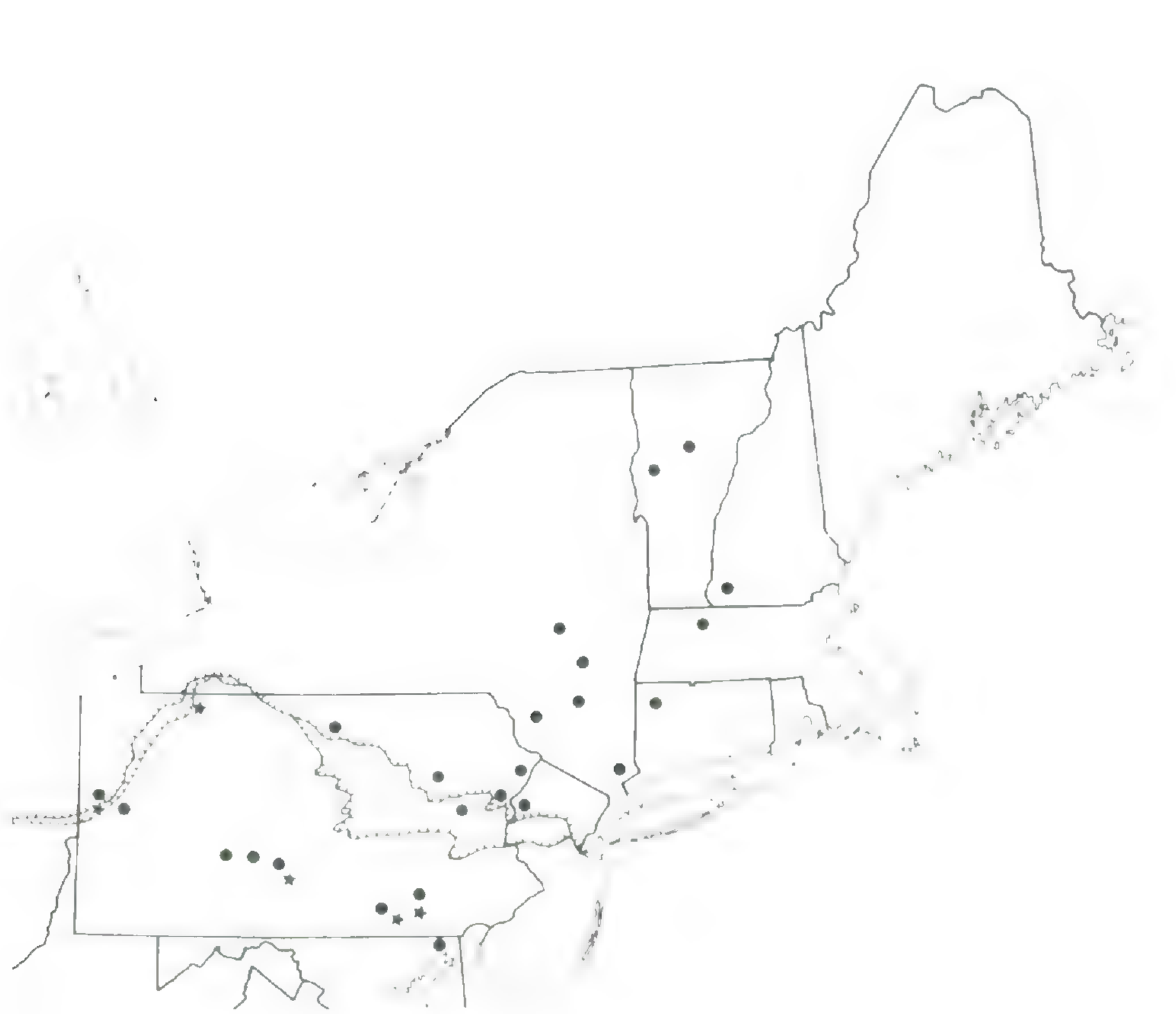

Figure 2. The known distribution of *Vittaria* (stars) and *Trichomanes* (dots) in the northeastern United States. Each symbol represents a county in which the plants were collected. Hatched lines represent the approximate southern limits of Wisconsin (upper line) and Illinoian (lower line) glaciation.

basis of its association with this forest type, a northern limit for *Trichomanes* may be predicted to occur in the mountains of southernmost Quebec.

Vittaria gametophytes were not found in any habitats covered by Wisconsin glaciation. They were found in habitats just beyond the southern terminus of Wisconsin glaciation, and in one site, approximately one kilometer within the boundary of Illinoian glaciation (Gray, 1960). Some *Vittaria* sites are as far north as glaciated sites harboring *Trichomanes* but not *Vittaria*. Since the two genera have nearly identical habitat requirements, frequently sharing the same habitat, it is reasonable to conclude that Pleistocene glaciation has influenced the current distribution of *Vittaria*.

In considering the origin of gametophytes of *Vittaria* and *Trichomanes*, it is important to analyze the nature of their habitats and probable means of dispersal. Their habitats are invariably situated within canyon-like topography and surrounded by a dense mature forest canopy. The microhabitats in which they grow are crevices or grottos deeply recessed under cavernous rock outcrops. Wind currents in these microhabitats are minimal so that wind dispersal of propagules into or out of these habitats seems unlikely. More plausible dispersal agents are the variety of insects and other invertebrates which actively seek out these same habitats.

Another aspect of their distribution suggests that they are not presently being dispersed beyond their immediate habitats. They are not found in man-made habitats such as roadcuts, tunnels, bridges or quarries, although these often present all conceivable combinations of light and moisture with appropriate substrate, and are in proximity to existing populations. Many such habitats have been in existence 100 years or more.

If the gametophytes are not currently dispersing and thus not invading adjacent available habitats, when did they reach their current northeastern distribution? In the case of *Trichomanes*, this was certainly post-Pleistocene, perhaps during a hypsithermal period (Cushing, 1965; Davis, 1965) when a warmer climate may have facilitated northward migration. At this time, sporophytes of *Trichomanes* may also have extended their distribution northward into this area and contributed to the spread of the gametophytes.

A pre-Pleistocene distribution of *Vittaria* appears to have been truncated by Pleistocene glaciation. This conclusion is evidenced by the coincident northern limits of the plants and southern limit of

glaciation from southern Indiana[1] to eastern Pennsylvania. This coincidence holds despite the fact that habitats near the more northerly areas of the glacial terminus appear much less favorable to warm temperate plants than do some more southerly habitats lying north of glaciation. For example, the high, exposed rim rocks of the Allegheny reservoir in unglaciated northwestern Pennsylvania support populations of *Vittaria* whereas the more protected narrow canyons and waterfalls of Rickets Glen and the Delaware Water Gap of glaciated cental and eastern Pennsylvania contain abundant *Trichomanes* but not *Vittaria.*

Could the absence of *Vittaria* within the glaciated area be attributed to glacial alteration of habitats rendering them permanently unsuitable for these plants? In the Appalachian Mountains there is little probability of this surmise as the mountain topography was not greatly altered by glaciation, and glacial drift has been largely removed from upland areas through subsequent erosion (Muller, 1965; Schafer and Hartshorn, 1965; Thornbury, 1965). Common acidiphilic fern associates of *Vittaria,* e.g. *Asplenium montanum,* and *Trichomanes* gametophytes, and mosses such as *Hookeria acutifolia* also show no limitations to unglaciated areas (Crum & Anderson, 1981; Wherry, 1942).

In glaciated areas west of the Appalachian Mountains, calcareous tills generally overlie sandstone outcrops of the type suitable for *Vittaria* in unglaciated areas (Goldthwait, et al., 1965; Wayne & Zumberge, 1965; Thornbury, 1965) and such outcrops are less frequent and less continuous than they are beyond the glacial terminus. These factors are significant, but do not alone explain the absence of *Vittaria* in this area. *Trichomanes* occurs in Montgomery County, Indiana, suggesting suitability of habitat there, approximately 25 km within Wisconsin glaciation. *Vittaria* occurs in Martin Co., approximately 100 km from the Montgomery Co. site and just beyond the Illinoian glacial boundary.

In Lawrence Co., Pennsylvania, *Vittaria* gametophytes occur in great abundance on Pottsville sandstone approximately 1 km within Illinoian glaciation and about 1 km beyond the Wisconsin glacial limit. Some post-Illinoian migration of the gametophytes has

[1]This study has yielded new county records for *Vittaria* gametophytes in Martin and Perry Counties, Indiana and Fairfield County, Ohio. It was previously known from Crawford County, Indiana and Hocking and Jackson Counties, Ohio.

obviously occurred, perhaps made possible by the continuity of suitable habitats along Slippery Rock Creek from this area to well south of glacial limits.

Similarly, in Hocking and Fairfield counties of Ohio, *Vittaria* is abundant on the common and continuous outcrops of Pottsville sandstone to within 1 km of the glacial terminus. However, it is absent from the relatively isolated outcrops of the same substrate in Licking Co., Ohio, 60 km to the northeast, although habitats here support populations of *Trichomanes* gametophytes, *Asplenium pinnatifidum*, and the acidophilous mosses *Hookeria acutifolia* and *Bryoxiphium norvegicum*, all frequent associates of *Vittaria*. These observations suggest that a large geographical extent and linear continuity of suitable habitats are important determinants of the occurrence of *Vittaria*, perhaps operating through probability of habitat continuity over time as well as provision of migration routes requiring minimal transport distances.

It is difficult to explain this distribution of the Appalachian *Vittaria* gametophytes except by assuming a very limited dispersal capacity and consequently a Pleistocene occurrence very near the glacial terminus. The latter is not unlikely considering the bryophyte-like growth form of *Vittaria*, its ability to tolerate freezing (Farrar, 1978), and the strong climatic moderation afforded by the cave-like habitats of these plants (Fig. 1). Similar rock shelters in Alabama, Illinois, and Missouri contain remains of human habitation which have been dated at more than 9000 years b.p. (Jennings, 1968). Clearly these habitats are stable and very likely persisted with little modification throughout the Pleistocene. In such habitats a frequent associate of *Vittaria* in the northern, unglaciated portions of the Appalachian Plateau is the sword moss, *Bryoxiphium norvegicum*. Steere (1937) described this moss as exhibiting a relict distribution pattern of a species which thrived near the periphery of pleistocene glaciers.

In summary, it seems likely that both *Trichomanes* and *Vittaria* reached pre-Pleistocene and possibly interglacial northern limits more or less coincident with the distribution of the Central Hardwood forests of eastern North America. *Trichomanes* has regained this distribution during post-Pleistocene time, possibly during an interval warmer than the present. *Vittaria*, by contrast, appears to have migrated very little beyond the areas to which it was restricted by Pleistocene glaciation. The greater post-Pleistocene migratory

success of *Trichomanes* may be related to the more northerly occurrence of sporophytes of this genus.

Many prospective northeastern sites for these ferns remain uninvestigated. *Trichomanes* may be expected wherever sizeable outcrops of non-calcareous rocks occur throughout the range indicated in Figure 2, and further significant range extensions are likely to be documented in the northeastern U.S. and possibly in southeastern Canada. *Vittaria* likely occurs throughout unglaciated Pennsylvania and possibly in unglaciated portions of New York and New Jersey. Our conclusions regarding the history and mobility of *Vittaria* do not exclude the possibility of its chance occurrence within the limits of Pleistocene glaciation.[2] However, present information strongly suggests that if found in such areas, *Vittaria* there will not approach the abundance or frequency of its occurrence in unglaciated areas.

LITERATURE CITED

Crum, H. A. & L. E. Anderson. 1981. Mosses of Eastern North America. Vol. 2. Columbia Univ. Press, New York.

Cushing, E. J. 1965. Problems in the Quaternary phytogeography of the Great Lakes region. *In:* Wright, H. E., Jr. and D. G. Frey, Editors. 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

Davis, M. B. 1965. Phytogeography and palynology of Northeastern United States. *In:* Wright, H. E., Jr. and D. G. Frey, Editors. 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

Farrar, D. R. 1967. Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the southern Appalachians. Science **155**: 1266–1267.

———. 1978. Problems in the identity and origin of the Appalachian *Vittaria* gametophyte, a sporophyteless fern of the Eastern United States. Amer. J. Bot. **65**: 1–12.

Goldthwait, R. P., A. Dreimanis, J. L. Forsyth, P. F. Karrow, & G. W. White. 1965. Pleistocene deposits of the Erie Lobe. *In:* Wright, H. E., Jr. and D. G. Frey, Editors. 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

Gray, C. 1960. Geologic Map of Pennsylvania. Pennsylvania Geological Survey, fourth series. Commonwealth of Pennsylvania, Harrisburg.

Jennings, J. D. 1968. Prehistory of North America. McGraw-Hill, New York.

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[2]Note added in proof: Collections of *vittaria* gametophytes have recently been made in Lake and Geauga Counties in northeastern Ohio by Allison Cusick of the Ohio Department of Natural Resources. The plants were collected from Sharon Conglomerate exposed along the Lake Erie watershed. This site is approximately 80 km north of the Wisconsin glacial terminus and constitutes the first documented occurrence of *Vittaria* within the boundaries of Wisconsin glaciation.

LITTLE, E. L., JR. 1971. Atlas of the United States Trees. Volume 1. Conifers and Important Hardwoods. U.S. Dept. Agric. Misc. Publ. 1146. Washington, D.C.

MCALPIN, B., & D. R. FARRAR. 1978. *Trichomanes* gametophytes in Massachusetts. Amer. Fern J. **68:** 97–98.

MULLER, E. H. 1965. Quaternary Geology of New York. *In:* Wright, H. E., Jr. and D. G. Frey, Editors. 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

SCHAFER, J. P. & J. H. HARTSHORN. 1965. The Quaternary of New England. *In:* Wright, H. E., Jr. and D. G. Frey, Editors. 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

STEERE, W. C. 1967. *Bryoxiphium norvegicum,* the sword moss, as a preglacial and interglacial relic. Ecology **18:** 346–358.

THORNBURY, D. 1965. Regional geomorphology of the United States. Wiley, New York.

WAGNER, W. H., JR., & R. A. EVERS. 1963. Sterile prothallial clones (Trichomanes?) locally abundant on Illinois sandstones. Amer. J. Bot. **50:** 623.

WAYNE, W. J., & J. H. ZUMBERGE. 1965. Pleistocene geology of Indiana and Michigan. *In:* Wright, H. E., Jr. and D. G. Frey, Editors. 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

WESTVELD, M. & COMMITTEE ON SILVICULTURE, NEW ENGLAND SECTION, SOCIETY OF AMERICAN FORESTERS. 1956. Natural forest vegetation zones of New England. J. Forestry **54:** 332–338.

WHERRY, E. T. 1942. Guide to Eastern Ferns. ed. 2 . Science Press, Lancaster, Pennsylvania.

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APPENDIX 1

LIST OF COLLECTIONS[1]

Vittaria[2]

PENNSYLVANIA: **Huntingdon Co.:** Orbisonia Gap, Juniata and Tuscarora sandstone, 81-9-20-6, 81-9-20-7. **Lancaster Co.:** Kelley's Run, Wissahickon schist, 81-9-22-6; Tucquan Glen, Wissahickon schist, 81-10-2-5. **Lawrence Co.:** McConnell's Mill Gorge of Slippery Rock Creek, Pottsville sandstone, 81-10-21-4. **Warren Co.:** Jake's Rocks on Allegheny Reservoir, Pottsville sandstone, 81-10-20-1. **York Co.:** Otter Creek, Wissahickon schist, 81-9-22-12.

Trichomanes[2]

CONNECTICUT: **Litchfield Co.:** Campbell Falls—gorge south of falls, schist, 81-10-17-2; Kent Falls, granite-gneiss, 81-10-17-3. MARYLAND: **Cecil Co.:** Susquehanna River—east side, 1 km south of Pa. state line, Peters Creek Schist, 81-9-23-1. MASSACHUSETTS: **Franklin Co.:** West of Mt. Toby along Hwy 47, 5 km north of Sunderland, Triassic conglomerate and shale, 81-10-16-1. NEW HAMPSHIRE; **Cheshire Co.:** Chesterfield Gorge, quartzite, 81-10-15-1. NEW JERSEY: **Warren Co.:** Delaware Water Gap – Van Campen's Brook, Bloomsburg shale and siltstone, 81-9-27-2. NEW YORK: **Green Co.:** 1 km south of Westkill on Hwy 42, Catskill sandstone, 81-10-10-1. **Schoharie Co.:** Minekill Falls, sandy shale, 81-10-10-3. **Sullivan Co.:** Frost Valley, Catskill sandstone, 81-10-9-5. **Ulster Co.:** Frost Valley, Catskill sandstone, 81-10-9-8. **Westchester Co.:** Mianus River Gorge, schist, 81-10-9-2. PENNSYLVANIA: **Blair Co.:** Bell's Gap, Pocono sandstone, 81-9-19-1. **Butler Co.:** Jennings Environmental Education Center, Pottsville sandstone, 81-10-21-1. **Cambria Co.:** Bell's Gap, Pocono sandstone, 81-9-19-3. **Carbon Co.:** Hickory Run, Pocono sandstone, 81-9-25-1. **Huntingdon Co.:** Juniata River – junction of US 22 and Pa 829, Catskill sandstone and shale, 81-9-20-1; Orbisonia Gap, Juniata sandstone, 81-9-20-5. **Lancaster Co.:** Kelly's Run, Wissahickon schist 81-9-22-8; Pequea River, Wissahickon schist, 81-10-2-8; Furnace Hills—Seglock Run, Triassic conglomerate and shale, 81-9-30-1. **Lawrence Co.:** McConnel's Mill—Gorge of Slippery Rock Creek, Pottsville sandstone, 81-10-21-7. **Luzerne Co.:** Rickett's Glen—Kitchen Creek Falls, Pocono sandstone, 81-10-18-1. **Monroe Co.:** Delaware Water Gap—Slateford Creek, Martinsburg shale, 81-9-27-1. **Pike Co.:** Bushkill Falls, Marine Bed shale and sandstone, 81-9-26-1; Dingman's Falls, Marine Bed shale and sandstone, 81-9-26-8. **Tioga Co.:** Colton Point—Pine Creek Gorge, Catskill sandstone, 81-10-19-1. **York Co.:** Susquehanna River at Accomac, Chickies quartzite. 81-9-30-1; Otter Creek, Wissahickon schist, 81-10-12-4. VERMONT: **Addison Co.:** 2 km west of Ripton, quartzite, 81-10-12-1; Moss Glen, schist, 81-10-12-2. **Washington Co.:** Mad River Glen, schist, 81-10-12-4.

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[1]Collection numbers are those of Farrar.

[2]All specimens are gametophytes only.

ADIANTUM PEDATUM SSP. *CALDERI*, A NEW SUBSPECIES IN NORTHEASTERN NORTH AMERICA

WILLIAM J. CODY

The presence, in the Shickshock Mountains of the Gaspé Peninsula, Quebec, of an *Adiantum* which differed substantially from *Adiantum pedatum* L. of rich deciduous woods in northeastern North America was pointed out by Fernald (1905). This plant he concluded was var. *aleuticum* Rupr., which is known from California to Alaska and eastern Asia. Rugg (1922) later reported it from Belvidere Mountain in northwestern Vermont, and Mousley (1923) reported it from Stanstead County, Quebec, and western Newfoundland.

An examination of some 300 sheets of *Adiantum pedatum* ssp. *pedatum* from eastern North America and over 100 sheets of *A. pedatum* ssp. *aleuticum* (Rupr.) Calder & Taylor from western North America has shown that the plants of the Shickshock Mountains and parts of southeastern Quebec and adjacent Vermont and western Newfoundland are even more distinct than ssp. *aleuticum* is from ssp. *pedatum*. They may be distinguished from ssp. *aleuticum* and ssp. *pedatum* by their generally shorter stature, stiffly crowded stipes, glaucous fronds, smaller pinnules and conspicuous indusia. The plants are found on serpentine and dolomite talus slopes and tablelands.

Of particular phytogeographic significance is the presence of similar plants on serpentine rocks in Washington and northern California. This distribution pattern is shared with another fern, *Polystichum scopulinum* (D. C. Eaton) Maxon.

The only specimen of *Adiantum pedatum* in the Linnaean Herbarium at London *(1252.2)* was collected by Kalm in Virginia. It is the typical plant of our northeastern North American woodlands, in which the fronds have arched and strongly recurved branches. The type material of ssp. *aleuticum* came from Unalaschka and Kodjak. A fragment of the Chamisso collection from Unalaschka has been seen (NY). It is the characteristic plant found from Alaska to California.

The following name is proposed for the plant of serpentine and dolmitic rocks:

Adiantum pedatum L. ssp. **calderi** *ssp. nov.*

A ssp. *pedato* et ssp. *aleutico* statura plerumque minore, stipitibus rigide aggregatis, frondibus glaucis, pinnulis semper parvioribus et indusiis conspicuis distinguendum. HOLOTYPE: cold sheltered ravines, Mt. Albert, Gaspé County, Quebec, *J. F. Collins & M. L. Fernald, s.n.* 14 August 1905 (DAO); ISOTYPE (GH) (Figure 1).

A chromosome number of $n = 29$ (det. G. A. Mulligan) has been obtained from a collection from Mount Albert (*C. Rousseau s.n.*, 5 Sept. 1965 (DAO)). This is the same as for both ssp. *pedatum* and ssp. *aleuticum*.

Many collections of this subspecies have been made by later collectors from the type locality, e.g. *Fernald & Collins 270* (GH, DAO), *Marie-Victorin 17000* (DAO), *Cody et al. 718* (DAO).

The following are additional localities. CANADA. **Quebec:** Megantic Co., Black Lake, en grosses touffes le long des ruisselets sur les terrains magnésiens découverts, *Marie-Victorin et al. 46, 653* (DAO) plus several other collections; Caribou Lake east of Black Lake, shaded serpentine, *Fernald & Jackson 11959* (CAN, GH); Caribou Hill, Black Lake, dry serpentine slopes and crests, *Fernald & Jackson 11957* (CAN, GH); Coleraine, sur les collines de serpentine depuis longtemps dénudées, *Marie-Victorin et al. 45, 434* (CAN); Thedford Mines, sur les serpentines près des mines, *Marie-Victorin et al. 4125* (CAN); Sherbrooke Co., Sawdust Lake, Chain Ponds, on rock ledges firmly rooted in narrow crevices, rocky bluff overlooking lake beneath young red pines (partly shaded), *Terrill 7970* (DAO); Wolfe Co., Lac Sunday, talus de'éboulis de serpentine, *Blais et al. 11,428* (DAO). **Newfoundland:** Humber District: Goose Arm, Parson's Cover, on dry limestone talus, *Rouleau 1751* (DAO); Serpentine (Coal) River, Red Barren Brook, dry serpentine shores, *Rouleau 1893* (DAO, CAN); North Arm, woods on southerly slopes of dry serpentine ridge, *Rouleau 872* (DAO); North Arm, Flagstaff Point, southerly slopes of dry serpentine ridge, *Rouleau 842* (DAO); Cloudy Pond Mountain, on the dry limestone talus, *Rouleau 200* (DAO, CAN); Bear Lake, limestone talus-slopes, *Rouleau 4584* (DAO, CAN); Rileys Brook, barren serpentine top of hill, *Rouleau 4423;* Blomidon Mountains, serpentine and magnesian limestone barrens, *Fernald & Wiegand 2308* (CAN); Benoit's River, Humber Arm, 48°58'N, 58°16'W, *Tuomikoski 426* (CAN); St. Barbe District: Bonne Bay, Stanleyville, on dry limestone talus, *Rouleau 443* (DAO, CAN); Trout River Big Pond, Rocky Brook, dry serpentine slopes, *Rouleau 3278* (DAO); Bonne Bay, the Tableland, dry serpentine barren slopes and tableland, *Rouleau 3773* (DAO, CAN); Gros Morne National Park, Trout River Pond, 49°17'N, 58°03'W, *Larix laricina* scrub with *Betula papyrifera* on serpentine talus slope, *Bouchard & Hay 73-5* (CAN); Gros Morne National Park, Winter House Brook, 49°28'N, 57°57'W, serpentine tableland, *Bouchard & Hay 73-4* (DAO); Bonne Bay, serpentine tablelands, *Fernald & Wiegand 2309* (CAN); St. Georges District: Bond Asbestos Mine, serpentine outcrop, *Rouleau 4436* (DAO, CAN); White Bay District: St. Anthony, east slope of Eastern White Hills, moist hillside, *Savile & Vaillancourt 2776* (DAO); Flatwater Pond, 49°48'N, 56°19'W, on rocky lake shore, *Shchepanek & White 2812* (CAN).

U.S.A. **Vermont:** Belvidere Mt., Eden, *Mrs. Jolley, s.n.* July 1922 (GH); Montgomery, *Mrs. Jolley, s.n.* in 1924 (GH). **California:** Gasquet, Del Norte Co., moist

Figure 1. Photograph of type specimen of *Adiantum pedatum* ssp. *calderi* (*Collins & Fernald*, Mount Albert, Quebec, 14 Aug. 1905 (DAO)).

spots in serpentine formation, *Tracy 9520* (DAO). **Washington:** Wenatchee National Forest, Mount Stewart, in crevice in moist draw on steep slope at foot of Esmerelda Peak, greenstone, *Cody 18454* (DAO).

The subspecies is named for James A. Calder, a former colleague and co-author of Flora of the Queen Charlotte Islands (Calder & Taylor, 1968), who pointed out the distinctiveness of this fern.

The following key may be used to separate the three subspecies of *Adiantum pedatum:*

A. Branches of fronds widely divergent, with the lowermost arched and strongly recurved (rich deciduous woods, northeastern North America) ..... ssp. *pedatum*

A. Branches usually strongly ascending

B. Fronds tightly clumped; pinnules glaucous, small, the middle 7–12 (17) mm long, but little incised; indusia conspicuous (serpentines and dolomites, western Newfoundland, Gaspé, Megantic and Sherbrooke counties Quebec, northern Vermont, California and Washington) .... ssp. *calderi* Cody

B. Fronds not tightly clumped; pinnules green, the middle larger (10) 12–20 (23) mm long, frequently deeply incised; indusia not conspicuous (rocky woods, Alaska to California)..... ssp. *aleuticum* (Rupr.) Calder & Taylor

The loan of specimens from National Museum of Natural Sciences, Ottawa (CAN), Gray Herbarium of Harvard University (GH), and New York Botanical Garden (NY), is much appreciated.

LITERATURE CITED

CALDER, J. A. & R. L. TAYLOR. 1968. Flora of the Queen Charlotte Islands, Part I. Systematics of the Vascular Plants. Canada Dept. Agriculture, Research Br. Monograph **4** Part 1. 659 pp.

FERNALD, M. L. 1905. An alpine *Adiantum*. Rhodora **7**: 190–192.

MOUSLEY, H. 1923. The alpine maidenhair fern (*Adiantum pedatum* L. var. *aleuticum* Rupr.) at Hatley, Stanstead County, Quebec. Can. Field-Nat. **27**: 84–85.

RUGG, H. G. 1922. *Adiantum pedatum* var. *aleuticum* in New England. Amer. Fern Jour. **12**: 128–129.

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CONTRIBUTIONS TO THE REPRODUCTIVE BIOLOGY OF PANAX TRIFOLIUM L. (ARALIACEAE)[1]

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Abstract: Flowering phenology, pollination, and morphological aspects of pollen and seeds of *Panax trifolium* L. are investigated. Plants are apparently androdioecious, but with very minor differences in pollen between floral forms (staminate and hemaphrodite). Light microscope and SEM studies were made of pollen and seeds.

Panax trifolium L. (Dwarf ginseng) is a springtime herb of eastern North America which perennates as a bulbous underground rhizome in moist forested areas. The genus is also represented in the region by the more economically important *Panax quinquefolium*. However, the latter is much less common due to over-collection for its reputed medicinal purposes.

There is relatively little information available concerning the biology of either species of *Panax*. What is available deals largely with *P. quinquefolium*[2] and is derived mostly from cultivated material, rarely from plants in their natural habitat (Hu, et al., 1980). Hu, et al. discussed the general ecology and habitat of both species but pointed out the lack of information concerning their growth habit, population structure and longevity of individuals. There are also few published reports for either species concerning field observations on flowering phenologies, breeding systems, and pollination.

Morphologically *Panax trifolium* is polygamous, with staminate and hermaphroditic flowers occurring on separate plants. The function of the gynoecium in the staminate flower is seldom questioned due to its very reduced nature; it completely lacks an ovary. However, the functionality of the pollen in the seed-producing hermaphroditic flowers is not as apparent and has not been investigated. A result of this lack of understanding is illustrated by the varied descriptions of sexual condition in the literature; "mostly unisexual" (Hu, et al., 1980), "dioeciously polygamous" (Fernald, 1950), and "often unisexual" (Gleason & Cronquist, 1963).

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[2]While this paper was in press another article dealing with *Panax quinquefolium* was published: Lewis, W. H., & V. E. Zenger. 1982. Population dynamics of the American Ginseng *Panax quinquefolium* (Araliaceae). Amer. J. Bot. **69:** 1483–1490.

The purpose of this paper is to report on investigations of several aspects of the reproductive biology of *Panax trifolium*. These include flowering phenologies, pollination, and morphological aspects of pollen and seeds. The results of these investigations suggest that *Panax trifolium* is androdioecious, a very uncommon and hence very interesting form of polygamy in which staminate and hermaphroditic flowers occur on separate plants (Lloyd, 1975; Charlesworth & Charlesworth, 1978).

MATERIALS AND METHODS

This study is based primarily on observations of two populations of *Panax trifolium* located in Durham, New Hampshire. For flowering phenologies 15 staminate and 15 hermaphroditic plants were selected, labelled with colored threads, and numbered. Each of these plants was then visited daily from 27 April to 4 June, 1981. Fruit development was subsequently followed in the same manner.

Observations of pollinators were made during the above visits to the populations. Floral insect visitors were collected by applying fine strands of Tanglefoot (The Tanglefoot Co., Grand Rapids, Michigan) to inflorescences of 10 plants of each type. The trapped insects were then collected the next day and preserved in 95% ethyl alcohol for later identification.

Pollinator exclusion experiments were conducted by covering 15 hermaphroditic plants with nylon screening before the flowers matured. The screens were removed after the flowering period and possible fruit development observed.

For pollen morphology studies, material was collected from both populations, acetolyzed (after Faegri & Iversen, 1975), rinsed twice with distilled water, and transferred to glycerine jelly. Microscope slides were then prepared from this material for light microscope (LM) observations. For scanning electron microscope (SEM) observations acetolyzed pollen was washed in two rinses of 100% acetone and transferred to aluminum stubs. The mounted material was then coated with approximately 200 angstroms of paladium gold.

Seeds were collected from each population for morphological studies. Observations were made of air dried seeds with a binocular dissecting microscope. For SEM observations air dried seeds were mounted on aluminum stubs using double-stick tape and coated

with paladium gold. All SEM observations were made on an AMR 1000 Scanning Electron microscope at the University of New Hampshire.

Descriptions of pollen and seeds are based on LM observations with supplemental information from SEM micrographs. All data in this study were evaluated statistically using an analysis of variance, or in the case of P/E ratios (pollen morphology), a Mann-Whitney U-test.

The amount of pollen produced per anther was estimated by counting all the grains in one sac and multiplying by two, pollen: ovule ratios were then calculated. Pollen was stained on glass microscope slides by dissecting open anthers in a drop of the respective stain (Analine blue, Aceto-carmine, and Malachite green-acid fuchsin). Cover glasses were then applied and observations made by examining most grains on the slide.

Investigations of herbarium material were made in three herbaria; Hodgdon Herbarium, University of New Hampshire (NHA), The New England Botanical Club Herbarium (NEBC) and the Gray Herbarium (GH) at Harvard University. Observations were made by examining each reproductive specimen and noting the sexual makeup of the inflorescence.

POLLEN MORPHOLOGY

Pollen grains of *Panax trifolium* are radially symmetrical, isopolar and tricoloporoidate, with three long, narrow colpi reaching nearly to the poles. The poroid areas are formed by a distinct zone of nexine thickening which incompletely surrounds a thinner area in the equatorial region of the colpus (Fig. 2, D,E). The regions of thickening form two separate semi-circular areas on opposite sides of the thin area and aligned parallel to the equatorial axis (Fig. 3, E). The poroid areas are approximately 4 to 5 μm in width, measured along the polar axis, and 5 to 6 μm in length, measured along the equatorial axis. The nexine is also thickened along the margins of the colpi (Fig. 2, G; Fig. 3, A), thus forming a margo that is apparent when the grain is expanded but is less distinguishable when the colpi are invaginated.

In cross section the tectate exine is composed of two distinct zones; the inner nexine and outer sexine (Fig. 2, C; Fig. 3, A, B).

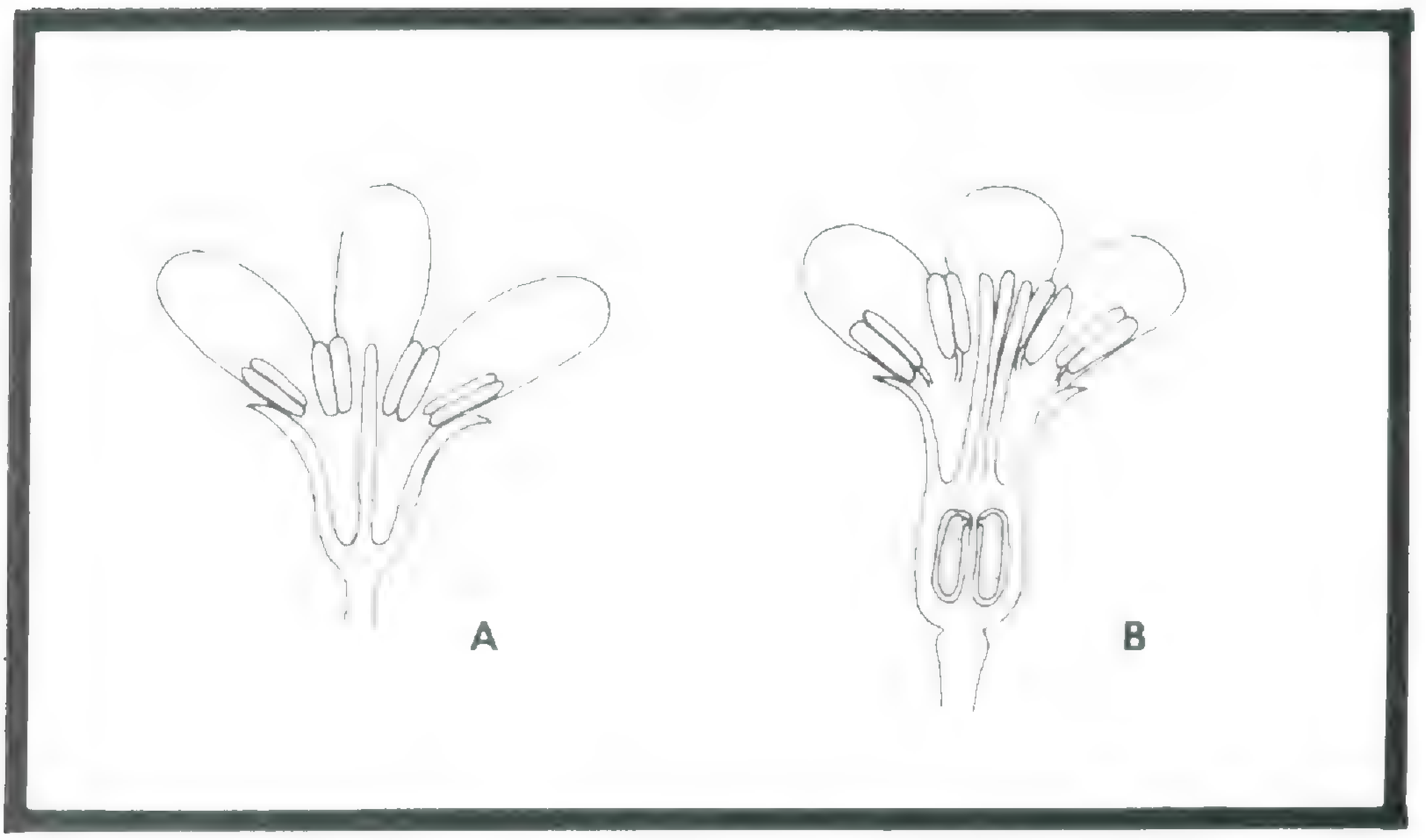

Fig. 1: Two floral types of *Panax trifolium:* A, staminate, B, hermaphrodite.

The nexine is approximately 1 μm in thickness throughout, excluding the previously described poroid regions. The sexine is thicker than the nexine (Fig. 2, C), ranging from about 2 μm in the center of the equatorial zone to approximately 3 μm in the central polar area. In both of these locations the sexine becomes thinner toward the colpi.

The sculpturing of the exine is difficult to distinguish through LM analysis alone. Different characters of the exine become apparent when LM observations are compared with those from the SEM. Under LM the grain surface appears reticulate (Fig. 2, A, B, F). SEM micrographs, however, illustrate a distinctly different striate tectum (Fig. 2, H,I; Fig. 3, B). This difference presumably results from a lack of

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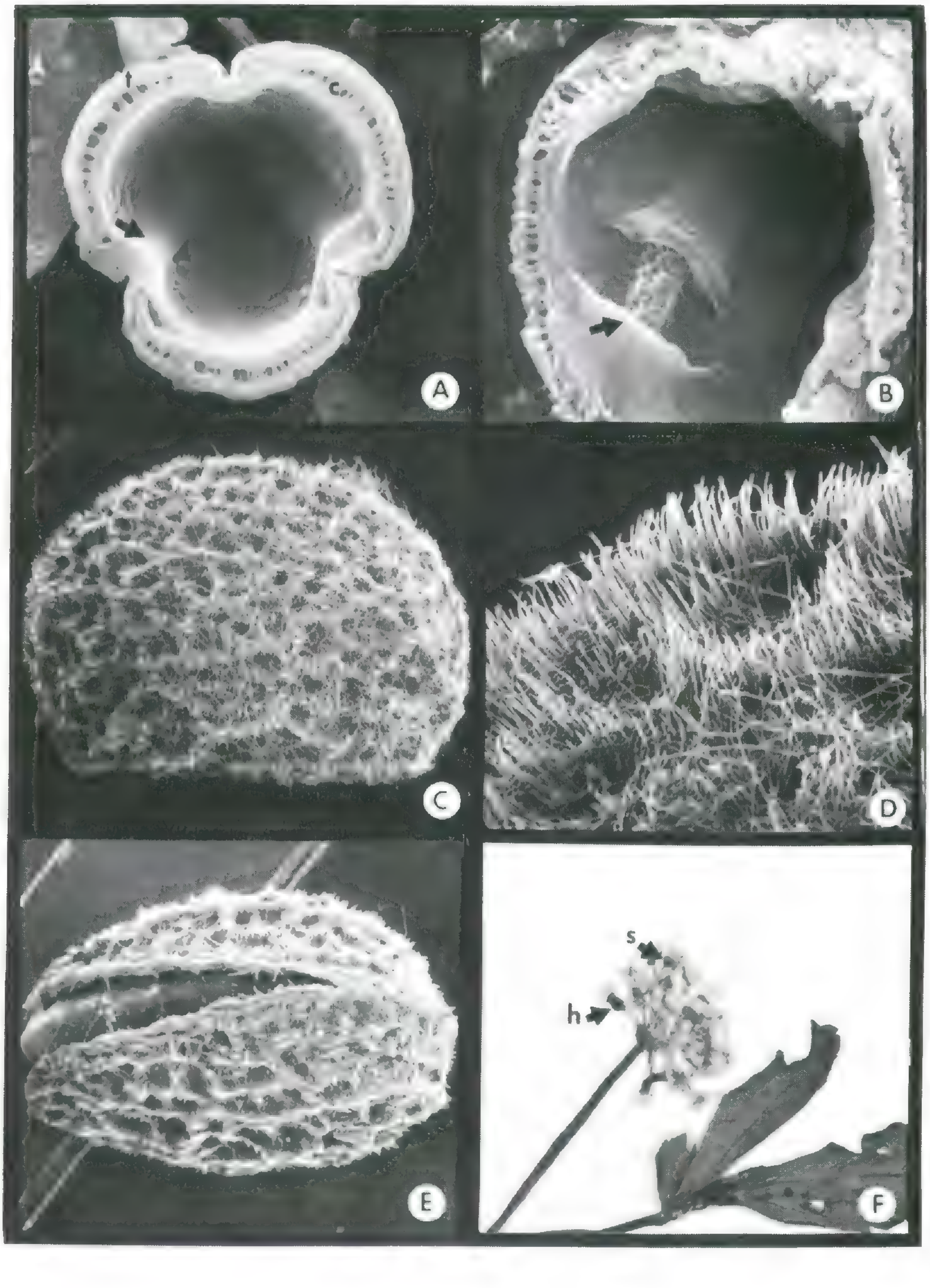
Fig. 2: **A — E,** series of LM micrographs focusing through a single grain in equatorial view. **A,** high focus showing columellae, appearing white (arrow) (1587×). **B,** slightly lower focus showing dark columellae (arrow) forming a reticulate appearance (1587×). **C,** optical cross-section of grain showing thin area of exine in the equatorial region (1587×). **D,** optical cross-section of poroid areas (1587×). **E,** surface view showing one colpus and poroid area (1587×). **F — G,** LM micrographs of grain in polar view. **F,** high focus showing white columellae (1587×). **G,** optical cross-section (1587×). **H — I,** SEM micrographs of separate grains in equatorial view. **H,** showing two invaginated colpi and the striate nature of the sexine (1235×). **I,** showing two colpi with slightly protruding colpus membranes in the poroid area (1100×).

A
B
C
D
E
F
G
H
I


A
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relief on the tectum, therefore causing it to appear more or less transparent under LM analysis. This phenomenon is illustrated in Kapp's (1969) LM description for grains of the species in which he reports the sexine to be reticulate. Thus the reticulate appearance is a result of the orientation of the subtending columellae (baculae), not the sculpturing of the tectum itself (Fig. 3, A, B). Very careful LM analysis shows faint striate sculpturing in the peripheral regions of some grains.

No distinct differences in exine sculpturing were found in pollen from the two floral types. However, upon comparison of size measurements some differences were revealed (Table 1). The mean equatorial axis lengths of grains from the two floral types were shown to be similar, but mean polar axis lengths were significantly different. Grains from hermaphroditic flowers exhibited slightly longer polar axis lengths on the average. Also, upon comparison of the ratios of polar to equatorial axis lengths (P/E ratio of Erdtman, 1952) significant differences were again shown (Table 1). Grains from the staminate flowers possessed P/E ratios ranging from 0.97-1.63 (suboblate-prolate) with a mean of 1.30 (subprolate). In comparison those from the hermaphroditic floral form ranged from 1.00-1.70 (prolate spheroidal-prolate) with a mean of 1.45 (prolate).

SEED MORPHOLOGY

Seeds of *Panax trifolium* are white and somewhat reniform in shape. The length ranges from 2.5 to 3.5 mm and the width from 1.5 to 2.5 mm (Table 1). The seed coat is characterized by a reticulate network of ridges, from which arise abundant short stiff unicellular hairs (Fig. 3, C, D).

Kapil, et al. (1980) state that seed hairs are usually adaptations for wind dissemination (anemochory), but note that they also function

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Fig. 3: **A — B,** SEM micrographs of sliced open grains. **A,** grain sectioned approximately in the equatorial plane showing the thickening of the nexine along the colpi (arrow), also showing the tectum (t) and columellae (c) (1655×). **B,** grain sectioned obliquely, showing the two separate nexine thickenings (arrow) parallel to each other in the equatorial zone (2330×). **C — E,** SEM micrographs of seeds. **C,** whole seed showing unicellular hairs high-lighting the reticulate pattern (10×). **D,** close-up of the seed coat showing the unicellular hairs (75×). **E,** whole seed showing split seed coat (15×). **F,** LM micrograph showing an andromonoecious inflorescence; staminate flower (m), hermaphrodite flower (h) (1.5×).

Table 1: **Data for comparison of characters of staminate and hermaphrodite individuals.**

Character	Staminate Plant				Hermaphrodite Plant				
	Range	Mean	S.D.	N=	Range	Mean	S.D.	N=	F-ratio (ANOVA)
No. of flowers per inflorescence	9–41	19.3	7.53	33	3–12	7.1	2.23	33	79.87
Total duration of inflorescence flowering (days)	12–19	14.5	2.46	15	5–8	6.0	1.15	15	97.78
Duration from anthesis to fruit maturation (days)	—	—	—	—	20–24	22.5	1.32	15	—
Pollen measurements;									
Polar axis (μm)	38–49	43.7	2.61	34	34–49	41.6	3.29	34	7.73
Equatorial axis (μm)	25–40	31.9	3.83	34	27–38	30.5	2.12	34	3.53
P/E ratio	0.97–1.63	1.30	—	34	1.00–1.70	1.45	—	34	—
No. of grains per anther sac (×2 for total no. in anther)	180–253	210	22.40	22	40–243	157	47.00	22	22.57
Percent stainability									
Analine Blue	—	99.3%	—	3	—	93.9%	—	3	—
Aceto-carmine	—	91.3%	—	3	—	99.7%	—	3	—
Mal Gr. / Ac. Fucs.	—	99.7%	—	3	—	97.3%	—	3	—
Flower size (μm)	1.0–1.5	1.2	1.75	30	1.5–2.5	1.30	0.25	30	149.76
Seed length (μm)	—	—	—	—	2.5–3.5	3.05	1.75	30	—

in water (hydrochory) and animal (epizoochory) dispersal. These mechanisms of dispersal do not seem to apply to the seeds of *Panax trifolium,* which fall to the ground and filter into the leaf litter.

Although the seeds of *Panax trifolium* germinate the next spring after they are shed, I have observed that the seed coat actually splits in the late fall (Fig, 3, E) (Table 2), not just before germination in early spring.

FLORAL MORPHOLOGY

The staminate flower of *Panax trifolium* (Fig. 1, A) is composed of a subconical floral tube which surrounds a persistent, reduced, solitary style. Five sepals and five petals alternate on the lip of the floral tube. Five two-celled anthers also arise from the margin of the floral tube opposite the sepals.

The hermaphroditic flower (Fig. 1, B) is composed of a cylindrical floral tube fused below to a three-carpellate inferior ovary which is noticeably swollen at its base. Three styles arise from the top of the ovary. Five sepals and five petals alternate on the lip of the floral tube, along with five two-celled anthers located opposite the sepals.

In the majority of cases the inflorescences of *Panax trifolium* are composed of only one or the other floral form: staminate or hermaphrodite. However, a survey of specimens located in several herbaria revealed that occasional andromonoecy exists; both staminate and hermaphroditic flowers on the same plant (Fig. 3, F). In a sample of 753 plant specimens, on approximately 260 sheets, 516 (69%) possessed only staminate flowers, 229 (30%) only hermaphroditic flowers and 8 (1%) had both flower types on the same inflorescence. I have not observed andromonoeceous individuals in the field.

FLOWERING PATTERNS AND SECONDARY SEX CHARACTERS

Two distinct plant types occur in *Panax trifolium.* One produces morphologically and functionally staminate flowers. These possess a full complement of five anthers as well as a single short style, but lack a noticeable ovary. The other plant type produces morphologically hermaphroditic flowers possessing one three-carpellate ovary, each carpel capable of producing a single seed. These flowers also contain the full five anther complement.

Table 2: **Pollen:ovule ratios; percent seeds with split seed coats; percent seed set; results of bagging.**

Percent seed set:

Total number of fruits collected: 154 from 22 plants.

Number with full (3/3) seed set 93 (60.4%)

Number with less than full seed set 61 (39.6%)

Percent seeds with split seed coat:

Date coll.	N=	Number with split seed coat	Number with non-split seed coat
4 Nov. 1981	53	34 (64.2%)	19 (35.8%)
30 Nov. 1981	33	31 (93.9%)	2 (6.1%)
23 Jan. 1981	16	13 (81.3%)	3 (18.7%)

Pollen:Ovule ratio:

$$\frac{\text{total no. grains per staminate flower}}{\text{total no. ovules per hermaphrodite flower}} = 696:1$$

$$\frac{\text{total no. grains per staminate and hermaphrodite flowers combined}}{\text{total no. ovules per hermaphrodite flower}} = 1220:1$$

$$\frac{\text{mean no. grains per staminate inflor.}}{\text{mean no. ovules per hermaphrodite inflor.}} = 986:1$$

$$\frac{\text{mean no. grains per staminate and hermaphrodite inflor.}}{\text{mean no. ovules per hermaphrodite inflor.}} = 2378:1$$

Seed set.

	No. seeds set	No. plants observed
Plants left uncovered (control)	25	10
Plants covered	0	15

Both plant types of *Panax trifolium* bloom concurrently within the population, with floral development and maturation taking place while the inflorescence is in a drooping position. Lloyd and Webb (1977) reported that staminate individuals of a dimorphic species often begin flowering before the seed-producing plant. I have not found this to be the case with *Panax trifolium*.

I have found several distinct differences between the two plant types (Table 3) that have been termed secondary sex characters (Lloyd & Webb, 1977). Distinct size differences of flowers, measured in bud, between the two plant types is obvious (Table 1; Fig. 3, F). This distinction is directly related to the presence of a fully developed ovary in one floral form and not in the other. Differences in numbers of flowers per inflorescence and their pattern of flowering were apparent. Significantly more flowers were observed on staminate inflorescences than on hermaphroditic, averaging 19 and 7 respectively (Table 1). The sequence of flowering of the staminate inflorescence was from the outermost flowers inward (centripetal), in contrast with the hermaphroditic inflorescences in which the flowers all opened more or less simultaneously. As a result of the differences in flowering patterns, the duration of flowering of the respective inflorescences differed markedly. Individual flowers, whether staminate or hermaphrodite, remained open for about four to five days. However, the entire staminate inflorescence blooms about twice as long as the hermaphrodite, averaging about 15 days for the staminate versus 6 for the hermaphrodite (Table 1). On the

Table 3: Secondary sex characters used in comparison of the two plant types.

1) Number of flowers per inflorescence.
2) Total duration of flowering per plant.
3) Sequence of flowering of respective inflorescence.
4) Amount of pollen produced per anther.
5) Percent stainability of pollen.
6) Flower size.

population scale this prolongs the total time that pollen is available and no doubt plays an important role in the pollination biology of the species.

During anthesis the staminate flower sheds its pollen and the anthers then fall. However, the perianth persists on these spent flowers and the flowers remain attached to the inflorescence until all the flowers have passed. After this time the inflorescence wilts and falls, or the entire stem dies. The persistent perianths may contribute to the attractiveness of the staminate inflorescence, drawing insects to the inner flowers that are still shedding pollen.

Anthesis proceeds very differently in the hermaphroditic flower. As the flowers open the anthers dehisce while the styles remain pressed together. After anther dehiscence, the styles begin to separate, becoming fully divergent after the anthers have fallen (protandry). Occasionally some overlap exists between the time of anther dehiscence and style divergence. The styles remain divergent for three to four days while pollination takes place. After this time they discolor and wilt slightly, after which the perianth is shed.

The significance of simultaneous blooming of the hermaphroditic inflorescence may be related to its protandrous nature. If non-simultaneous flowering occurred, selfing between flowers within an inflorescence (geitonogamy) would be more likely to take place. The simultaneous nature of flowering may increase the probability of outcrossing. At the time of stigma divergence there would be a better chance that all the pollen had been shed and the probability of outcrossing would be increased. Cruden (1977b) reported this same character in protandrous umbelliferous taxa.

The staminate plant often lives for only a few days after anthesis. Due to the fruit development period, the hermaphroditic stem persists well past anthesis. The initiation of fruit development, indicated by ovary expansion, begins very soon after the styles have wilted, often before the entire perianth has fallen. The time from style wilting to fruit maturation and drop averaged 28 days (Table 1). In many cases fruits which lacked the full three seed complement were observed (Table 2). It is not known whether this lack of seed set is related to an insufficient pollen or nutrient supply or to some other factor. Upon maturation the fruit becomes slightly yellow and falls from the plant, a result of an apparent abscission zone at the base of the ovary. On the ground the fruit wall quickly breaks down,

often along the septations between carpels. The seeds then fall from the fruit, sometimes forming small piles where several fruits have fallen together. My observations differed from those of Hu, et al. (1980) where they observed seeds being expelled from the fruits while the latter were still attached to the plant. After the fruits have fallen the stem lives for several more days, turns yellow and dies. Once shed, the seeds filter down into the litter. Germination takes place early the following spring.

Differences also exist between the two floral types regarding the amount of pollen produced per anther; the staminate producing approximately 25% more pollen per anther than the hermaphrodite (Table 1). Although less pollen is produced in the hermaphroditic flowers, that which is produced seems significant in amount and therefore should be considered when assessing pollen flow within the population. The staining qualities of the pollen from the two types also differed somewhat. When stained, pollen from staminate flowers consistently showed a higher staining percentage (less grain abortion), about 100% for staminate and 95% for hermaphroditic (Table 1). I prefer to use the phrase "staining percentage" rather then "viability percentage" because the staining characteristics of pollen are only an estimate of viability, not a definitive test.

Although the observations were not quantified and were somewhat inconsistent, there seemed to be differences in the degree to which the different grains took up the stain: the grains from staminate flowers often stained slightly darker than those from the other floral type. These slight differences could signify fertility differences and are therefore noteworthy.

If the breeding system of *Panax trifolium* is one of functional dioecy, distinct differences between functional versus non-functional pollen produced by the two floral types would be expected. Barrett and Helenurm (1981) reported that the anthers of the functionally female flowers of *Aralia nudicaulis* did not produce pollen, and Bawa (1977) found that anthers in similar functionally female flowers of *Cupania guatemalensis* produced pollen, but that anther dehiscence failed to occur. Anderson and Gensel (1976) and Anderson (1979) reported the lack of aperture development in pollen from what were interpreted as functionally female flowers of a species of *Solanum*. I have not observed any of these phenomena in *P. trifolium* other than the size differences noted earlier in the discussion of pollen morphology.

POLLINATION AND SEX RATIOS

Although not referring to dimorphic taxa, Cruden (1977a) illustrated a relationship between the ratio of pollen grains to number of ovules in a flower and its pollination mechanism. The more haphazard the mechanism the higher the pollen/ovule (P/O) ratio. This ratio can be estimated variously for *Panax trifolium* (Table 2). However, even in the estimate resulting in the largest ratio (2378.1), this ratio is still relatively small and suggests a rather predictable pollination mechanism. This agrees with the observations of pollinators made throughout this study.

Pollination in the species appears to be primarily entomophilous. Members of the insect families Empididae, Scatopsidae, and Syrphidae (Diptera) were observed visiting, and were collected upon, flowers of *P. trifolium*. Members of the Syrphidae were observed visiting the staminate flowers, where they initially collected pollen from several anthers, cleaned themselves of excess pollen and then reached to the base of the floral tube for an apparent "drink of nectar." This series of events was seen on several occasions and was also observed, but in less detail, on hermaphrodite flowers.

During early morning visits to the populations mosquitos were often seen sitting on flowers of *Panax trifolium* as well as those of *Coptis groenlandica* and *Anemone quinquifolia*. Although mosquitos are known to take part in pollination of some orchids (Stoutamire, 1968, 1971) these insects were never observed visiting the reproductive organs of *P. trifolium* flowers and were presumably only "resting."

A random walk through one population revealed a sex ratio highly skewed to staminate individuals; 110 staminate versus 16 hermaphrodite (approximately 7:1). This, combined with the higher numbers of flowers in staminate versus hermaphrodite inflorescences, indicates a relatively high pollen to ovule ratio at the population level. More detailed investigations into this phenomenon are required before the true significance of this ratio can be appreciated.

As a result of caging experiments in which 15 hermaphroditic plants were covered with nylon screening it was shown that significant anemophily probably does not occur (Table 2). In all cases no fruit development occurred on the covered plants whereas all uncovered plants in the same area exhibited significant seed set. This also

rules out mechanical self pollination but not necessarily self incompatibility.

CONCLUSION

The results of these investigations suggest that the pollen produced in the hermaphroditic flower appears functional, although possibly to a lesser extent than that from the strictly staminate flower. This, combined with the protandrous nature of the hermaphrodite flower, suggests that androdioecy may better characterize the breeding systems of *Panax trifolium* than previous designations. However, actual confirmation of androdioecy will not be accomplished until detailed crossing experiments within and between the two plant types are completed.

Panax trifolium is unique in that it exhibits ideal characters needed to conduct a survey regarding age structure of staminate and hermaphroditic plants in a population. During the growing season rhizomes of staminate and hermaphrodite individuals can be uncovered and their age determined by counting the persistent leaf scars. This allows a unique opportunity to estimate the longevity of the sexes, usually a very difficult undertaking. During the spring of 1981 a rhizome of *P. trifolium* was excavated which possessed approximately 30 leaf scars on a portion about 4 cm in length. Because one leaf is produced per year the plant was therefore about 30 years old.

The results of this study make a contribution to the current knowledge of several aspects of the reproductive biology of *Panax trifolium*. However, there remain many additional areas of investigation which have yet to be addressed, regarding among others, sex ratios, confirmation of pollen fertilities, self-compatibilities, and population age structure.

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LITERATURE CITED

ANDERSON, G. J. 1979. Dioecious *Solanum* species of hermaphroditic origin is an example of broad convergence. Nature **282:** 836–838.

———., & P. G. GENSEL. 1976. Pollen morphology and the systematics of *Solanum* section *basarthrum*. Pollen et Spores **18:** 533–552.

BARRETT, S. C. H. & K. HELENURM. 1981. Floral sex ratios and life history in *Aralia nudicaulis* (Araliaceae). Evolution **35:** 752–762.

BAWA, K. S. 1977. The reproductive biology of *Cupania guatemalensis* Rudbk. (Sapindaceae). Evolution **31:** 52–63.

CHARLESWORTH, B. & D. CHARLESWORTH. 1978. A model for the evolution of dioecy and gynodioecy. The Amer. Natur. **112:** 975–997.

CRUDEN, R. W. 1977a. Pollen-Ovule Ratios: A conservative indicator of breeding systems in flowering plants. Evolution **31:** 32–46.

———. 1977b. Temporal dioecism: An alternative to dioecism? Evolution **31:** 863–866.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm.

FAEGRI, K. & J. IVERSEN. 1975. Textbook of Pollen Analysis. Hafner Press, NY.

FERNALD, M. L. 1950. Gray's Manual of Botany. eighth edition. D. Van Nostrand, Co., NY.

GLEASON, H. A. & A. CRONQUIST. 1963. Manual of Vascular Plants of Northeast United States and Adjacent Canada. D. Van Nostrand Co., NY.

HU, S. Y., L. RUDENBERG, & P. DEL TREDICI. 1980. Studies of American Ginsengs. Rhodora **82:** 627–636.

KAPIL, R. N., J. BOR & F. BOUMAN. 1980. Seed appendages in Angiosperms. I. Introducton. Bot. Jahrb. Syst. **101:** 555–573.

KAPP, R. D. 1969. How to know Pollen and Spores. Wm. C. Brown Co., Dubuque, Iowa.

LLOYD, D. G. 1975. The maintenance of gynodioecy and androdioecy in angiosperms. Genetica **45:** 325–339.

———., & C. J. WEBB. 1977. Secondary sex characters in plants. Bot. Rev. **43:** 177–216.

STOUTAMIRE, W. P. 1968. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). The Mich. Bot. 7: 203–212.

———. 1971. Pollination in Temperate American Orchids. *In:* Proceedings of the sixth World Orchid Conference, Sydney, Australia, 1969. ed. M. J. G. Corrigan, Halstead Press.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
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MOUNTAIN LAUREL (*KALMIA LATIFOLIA* L.) DISTRIBUTION IN MASSACHUSETTS

BRAYTON F. WILSON AND JOHN F. O'KEEFE

ABSTRACT

Mountain laurel (*Kalmia latifolia* L.) presence along roads was mapped extensively for the whole state and intensively for selected quadrangles. Presence of mountain laurel in selected forests was determined from plots along transects. Frequency of mountain laurel was calculated as the per cent of road distance mapped, or of plots taken, that had laurel present. Mountain laurel occurred throughout the state on a range of sites, except for Cape Cod and eastern Plymouth County, in the high Berkshires and in the far west and north-west. Mountain laurel was uncommon in eastern Massachusetts and in a north-south strip through central Massachusetts, but was otherwise abundant. Absence of mountain laurel was probably due to either fire history, maritime influence, cold winters, or basic soils. Low frequencies were probably due to a previous history of extensive land clearing for agriculture.

Mountain laurel (*Kalmia latifolia* L.) is an evergreen shrub widely distributed in Massachusetts (Ebinger, 1974) even though it is near its northern limit (Kurmes, 1967). We have studied the details of local distribution related to site factors in central Massachusetts (O'Keefe, 1981). Our objective in the present study was to survey the whole state of Massachusetts to see where mountain laurel grows naturally. Our primary method was to map mountain laurel visible from automobiles while driving when deciduous species were leafless and the evergreen mountain laurel was conspicuous. We mapped the whole state on small scale maps and portions of the state on larger scale maps. We also incorporated data from site studies that used plots along transects in various forests. The results of the mapping and plot studies were then combined to interpret state-wide variations in the occurrence of mountain laurel.

METHODS

We mapped mountain laurel from November to April in 1979–1980 and 1980–1981. One person drove at 40–60 km/hr and observed mountain laurel on both sides of the road, the other helped observe and marked mountain laurel presence on maps. The extensive survey of state-wide distribution used USGS 1:250,000 maps; the intensive survey of portions of the state used USGS 1:24,000

maps (quadrangles). The resolution of the surveys, the minimum distance between mountain laurel plants that permits individual marks on the map rather than marking as continuous cover, was approximately 500 m for the extensive survey and 50 m for the intensive survey. For extensive mapping we tried to select representative roads that sampled the non-urbanized areas of the state. For the intensive survey we selected quadrangles within easy distance of Amherst, MA and drove on all of the passable roads in each quadrangle.

The per cent of mountain laurel on maps was determined by measuring on the maps the total distance marked as having mountain laurel and dividing by the total distance mapped. The extensive survey mapped only roads outside urbanized areas (yellow on the 1:250,000 maps). The intensive survey mapped only roads through wooded areas (green on the 1:24,000 maps). These percentages are only for comparative purposes on maps of the same scale.

Plot data from forests were taken at regular intervals along equally spaced transects that sampled the entire forest. Data from Monroe and Hawley-Savoy State Forests are from a study by Hibbs (1978) using 0.01 ha plots. Data from the other 6 forests came from a study by O'Keefe (1981) using 0.02 ha plots.

RESULTS

In the extensive survey we mapped about 1,800 km of road and 21% had mountain laurel. The state was composed of regions of differing mountain laurel distribution (Fig. 1, Table 1). As generally noted by others (Ebinger, 1974), we found no mountain laurel on Cape Cod or eastern Plymouth County. In eastern Massachusetts, roughly east of Worcester and an urbanized area, mountain laurel was scarce, although it was observed on a few rocky hills to the north and in some swampy areas to the south. Mountain laurel was common (about 40%) west of Worcester to the Connecticut River (region III) and in the Berkshires (region V), with the marked exception of a north-south strip in western Worcester county and south of the Quabbin reservoir west to the Connecticut river. There, mountain laurel was scarce generally, although it was locally abundant in some swampy areas and pond margins. Mountain laurel was less common in the northern Berkshires than in the southern Berkshires. In far western Massachusetts, the northern Housatonic valley, Hoo-

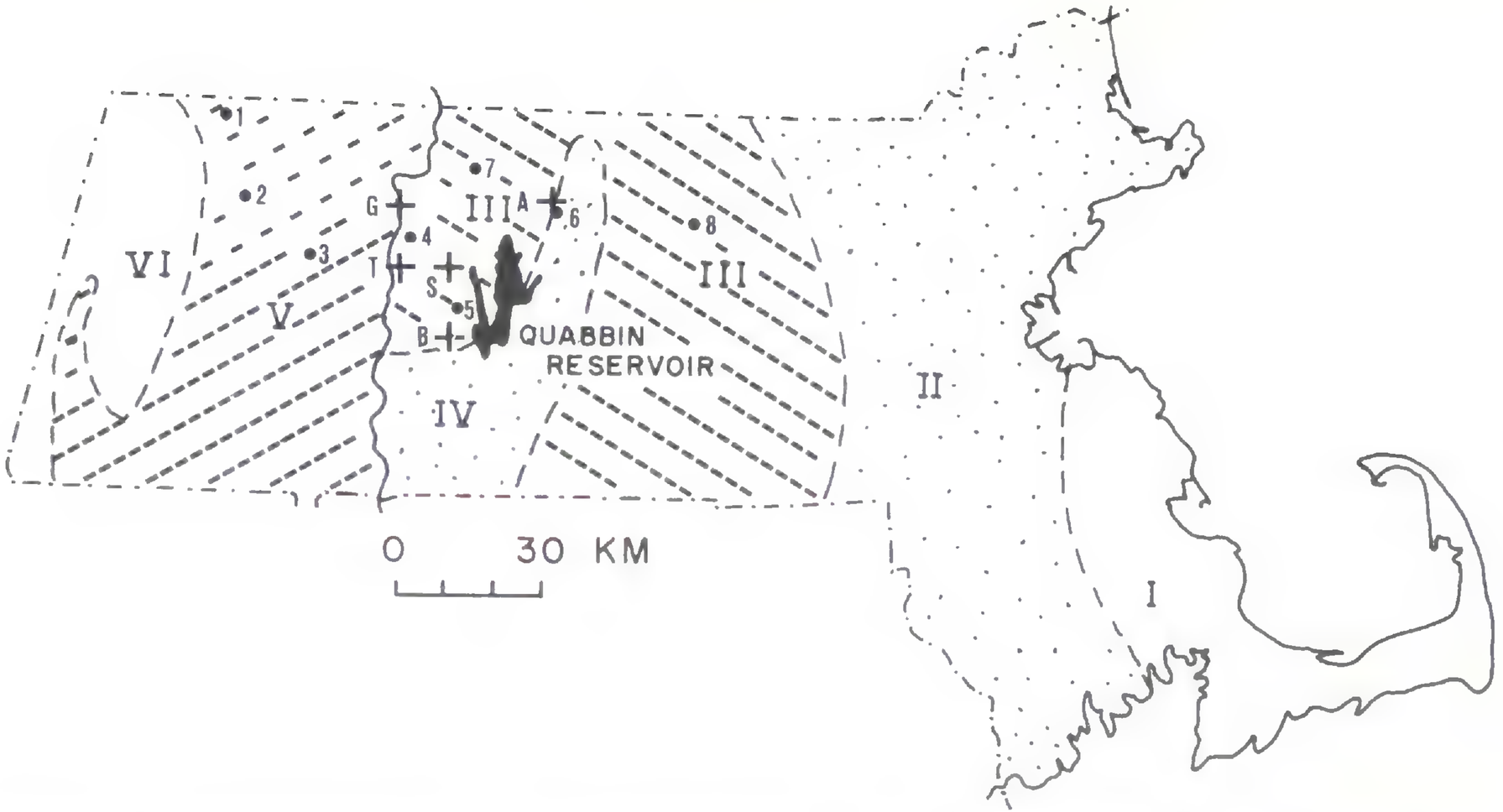

Figure 1. Distribution of mountain laurel in Massachusetts. The center of each quadrangle intensively mapped is marked by a + and identified with a letter (G = Greenfield, T = Mt. Toby, S = Shutesbury, B = Belchertown, A = Athol). Forests sampled with plots are marked by numbers (1 = Monroe, 2 = Hawley-Savoy, 3= D.A.R., 4 = Mt. Toby, 5 = Cadwell, 6 = Harvard, 7 = Erving, 8 = Leominster). Blank areas (I and VI) had no mountain laurel, stippled areas (II and IV) had mountain laurel, but it was uncommon, in hatched areas (III and V) mountain laurel was common at least along roads.

Table 1. Distribution of mountain laurel in different regions of Massachusetts. See Figure 1 for boundaries of the regions.

Region		% mountain laurel	Total km mapped
I	Cape Cod and E. Plymouth County	0	157
II	Eastern Mass.	3	506
III	E. Worcester County and N. of Quabbin Res.	38	303
IV	W. Worcester County + S. of Quabbin Res.	2	161
V	Berkshires	45	367
VI	Far west	8	212

sic valley, and Mount Greylock to the north, and the Taconic range along the New York border had no mountain laurel. Mountain laurel does occur on parts of a rocky ridge that extends north into the Housatonic valley south of Pittsfield (Fig. 1).

Greenfield, Mt. Toby, and Shutesbury quadrangles were all in region III where mountain laurel was abundant. They had about 40% mountain laurel along the roads (Table 2). The Mt. Toby quadrangle has about 50% agricultural land in the Connecticut river valley, therefore the total distance mapped is lower than in the other two quadrangles, but the percentage of mountain laurel in the wooded portions of the three quadrangles was about the same (Table 2).

Belchertown and Athol quadrangles were primarily in region IV where mountain laurel was scarce. The intensive survey found only 11–14% mountain laurel in these quadrangles. The Athol quadrangle showed a sharp discontinuity between the southwest corner, where mountain laurel was very abundant, and the rest of the quadrangle where it was scarce (Table 2). This discontinuity was along the boundary between regions III and IV (Fig. 1) where mountain laurel was respectively abundant and scarce. In the areas where mountain laurel was generally scarce in the Athol quadrangle it was locally abundant in, or near, a few swampy areas.

Three of the quadrangles could be subdivided into different physiographic areas (Table 2). The Greenfield quadrangle contains the Montague sand plain, an area of deep sands, frequently burned, with pitch pine (*Pinus rigida*) and scrub oak (*Quercus ilicifolia*)

stands similar to Cape Cod. Although mountain laurel was scarce on the sand plain, it did grow there. The Mt. Toby quadrangle contains extensive, flat, wooded swamps on the west side of the Connecticut river. Mountain laurel was just as abundant in these swamps as in the rest of the wooded portion of the quadrangle, predominantly rocky hills. In the Belchertown quadrangle mountain laurel was equally common in the rocky Pelham hills, where it is very dense in some areas, and in the valley floors of Granby and Belchertown. The Shutesbury quadrangle is almost entirely rocky hills and mountain laurel was abundant on the whole quadrangle.

The data for mountain laurel occurrence in State Forests (Table 3) are not biased towards roadside observations as are the maps. Generally the data from plots were consistent with the location of the forest in the regions of the state delineated by the extensive mapping. Both Monroe and Hawley-Savoy State Forests are at high altitudes (700 800 m) in the northern Berkshires and neither had any mountain laurel. The D.A.R. state forest is in the central Berkshires, at lower elevation (500m) and 13% of the plots had mountain laurel. The Harvard Forest is in region IV, where mountain laurel is

Table 2. Distribution of mountain laurel in selected quadrangles. See Figure 1 for location of quadrangles.

Quadrangle	% mountain laurel	Total km mapped
Greenfield	36	72
Sand plain	3	5
Remainder	38	67
Mt. Toby	37	35
Swamp	38	11
Remainder	34	24
Shutesbury	42	58
Belchertown	14	63
Hills	14	50
Valleys	14	13
Athol	11	88
SW corner	64	11
Remainder	3	77

Table 3. Distribution of mountain laurel in selected forests. Numbers of the forests refer to their numbers on Figure 1.

Forest	% mountain laurel	Total number of plots
1 Monroe	0	191
2 Hawley-Savoy	0	213
3 D.A.R.	13	270
4 Mt. Toby	34	395
5 Cadwell	32	620
6 Harvard	10	615
7 Erving	41	470
8 Leominster	79	370

scarce, and it had only 10% mountain laurel. The other forests are in region III where mountain laurel was abundant and all had more than 30% of the plots with mountain laurel. In many parts of Leominster state forest, where mountain laurel was the most abundant we encountered, the mountain laurel formed almost impenetrable thickets covering many hectares.

DISCUSSION

Mountain laurel grows naturally in most of Massachusetts, with three exceptions. We did not observe it on Cape Cod or eastern Plymouth County, in the high portions of the northern Berkshires, or in northwestern Berkshire county and the Taconic range. It is generally assumed that mountain laurel is absent from Cape Cod due to the past history of severe fires. In Rhode Island, fire eliminated large mountain laurel and greatly reduced the relative density of small ones (Brown, 1960). We did observe mountain laurel growing on a site similar to Cape Cod, the Montague sand plain, where fires are common, so additional maritime factors may be important on Cape Cod. Mountain laurel presumably cannot grow in the high Berkshires because of the cold winters. It does occur throughout most of the Berkshires at lower elevations. Limitation by the cold winters is also consistent with the fact that the northern limit for the species is in southern Vermont and New Hampshire. The lack of mountain laurel in northwestern Berkshire county is probably related to the general decreased acidity of the soil (USDA, 1973). Mountain laurel generally prefers acid soils (Braun, 1961).

Within those areas of Massachusetts where mountain laurel grows it can be found on almost any site, from deep sands, to swamps, to rocky hillsides. Yet, despite its adaptability, it is uncommon both east of Worcester and in a strip through western Worcester county and south of the Quabbin reservoir. In both areas where it is generally uncommon it can still be locally abundant.

The major factor that probably makes mountain laurel generally uncommon in some areas is land use history. If land has been cleared of forest, mountain laurel is extremely slow to re-invade when the land is abandoned (O'Keefe, 1981). Mountain laurel has stringent seed bed requirements, usually moss, and the seeds do not spread far from the parent plant (Kurmes, 1961). As a result, mountain laurel is usually found either in or near areas that were never cleared of forest during the height of agriculture in the 1800's (O'Keefe, 1981). Consequently, mountain laurel can provide a clue to past land use, but it is not, by itself, an adequate indicator of non-cleared land. For the same reason, mountain laurel may be abundant locally in swamps or on rocky slopes that, because they were never cleared, served as refugia for the mountain laurel. The eastern part of the state is, and has been, highly populated and relatively flat so most of the land has probably been cleared and mountain laurel distribution is severely restricted. The strip in central Massachusetts where mountain laurel is scarce is not highly populated, but it was extensively cleared in the 1800's (Raup & Carlson, 1943). In the area of the Brookfields, south and east of the Quabbin rerservoir, there are still a large number of farms on top of the rolling hills. The present distribution of mountain laurel at the Harvard Forest coincided almost exactly with land that was never cleared in the past (O'Keefe, 1981). There may be other factors limiting mountain laurel distribution in this central portion of the state, but land use history is probably the major factor.

It is difficult to determine the overall bias introduced by the mapping techniques used in this study. A survey from automobiles gives a sample that is potentially biased in several ways: small plants cannot be seen from moving automobiles, the edges of roads have relatively high light intensities that favor the growth of mountain laurel, road banks may create favorable seeds beds for mountain laurel establishment, roads tend to pass through populated areas with more intensive land use history, roads tend to be in valleys rather than on hill tops. Interstate highways avoid some of these

biases, but there are not enough of them and it is unsafe to drive slowly. Mountain laurel undoubtedly grows in some areas where we saw none from the roads. The results of mapping in this study agree quite well with the results of studies using plots, so we assume that the bias introduced by the mapping technique is relatively unimportant.

ACKNOWLEDGMENTS

We thank Mark Dale, Anne Hine, Gary Kronrad, Karen Saunders, and Mary Alice Wilson for assistance in mapping. Supported by Massachusetts Agricultural Experiment Station Grant McIntire-Stennis 32.

LITERATURE CITED

Braun, E. L. 1961. The Woody Plants of Ohio. Ohio State Univ. Press, Columbus.

Brown, J. H. 1960. The role of fire in altering the species composition of forests in Rhode Island. Ecology **41**: 310–316.

Hibbs, D. E. 1978. The life history and strategy of striped maple (*Acer pensylvanicum*). Ph.D. Thesis, University of Massachusetts, Amherst.

Ebinger, J. E. 1974. A systematic study of the genus *Kalmia*. Rhodora **76**: 315–398.

Kurmes, E. A. 1961. The ecology of mountain laurel in southern New England. Ph.D. Thesis, Yale University, New Haven, Connecticut.

———. 1967. The distribution of *Kalmia latifolia* L. Amer. Midl. Nat. **77**: 525–527.

O'Keefe, J. F. 1981. Factors affecting the distribution and growth of mountain laurel (*Kalmia latifolia* L.) in central Massachusetts. MS Thesis, University of Massachusetts, Amherst.

Raup, H. M. & R. E. Carlson. 1941. The history of land use in the Harvard Forest. Harvard Forest Bull. **20**.

USDA. 1973. General soils report, Berkshire County. USDA Soil Cons. Ser. with Berkshire-Franklin Resource Dev. Project.

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NEW ENGLAND NOTE

TRIPHORA TRIANTHOPHORA IN MASSACHUSETTS AND VERMONT

PETER F. ZIKA

Triphora trianthophora (Swartz) Rydberg is a small and inconspicuous orchid that flowers in mid to late August and fruits in September in southern Vermont. *Triphora* reaches the northern limit of its range in New England. Crow et al. (1981) classify *Triphora* as rare in New England but not threatened or endangered. Coddington & Field (1978) included the species on the Massachusetts list of rare and endangered plants. There is one historical Massachusetts station, from Conway, Franklin County, where the species was last collected in 1928 (*Allis s.n.*, AMES). *Triphora* is also on the Vermont rare and endangered list (Countryman, 1978). All Vermont records are from Windham Co., the southeast corner of the state, where *Triphora* was last collected in 1903, in Dummerston, (*Howe s.n.*, VT). Vermont also has documented historical stations from Brattleboro and Newfane. Rugg (1950) reported the Brattleboro station was last seen circa 1925 and described a station he discovered in 1943 in Brookline, Vermont.

Photographs of plants from each of the four known extant *Triphora* populations in Massachusetts and Vermont were made in 1981 and are on deposit in the Pringle Herbarium (VT).

MASSACHUSETTS: FRANKLIN COUNTY

Greenfield. Station discovered by the author in 1981. Two plants, one in flower on 19 August.

VERMONT: WINDHAM COUNTY

Brattleboro. Roberta Poland and Herman Willey provided directions to find this colony. Seventeen plants total, fourteen flowering on 18 August, three fruiting on 20 September.

Brookline. This is Rugg's 1943 station. Roberta Poland guided the author to the site. Thirteen plants, seven flowering on 18 August.

Dummerston. Station discovered by Roberta Poland in 1981. Eleven plants, ten flowering on 18 August, six fruiting on 19 September.

At each *Triphora* station the habitat was strikingly similar: an old-age or maturing forest, dominated by *Tsuga canadensis* (L.) Carriere and *Fagus grandifolia* Ehrhart. At the Massachusetts station the beeches were the largest trees, averaging 9–inch DBH. In Brookline the largest trees were hemlocks, averaging more than 14–inch DBH. Other prominent woody species in the woodlots were *Acer saccharum* Marshall, *Acer rubrum* L., and *Ostrya virginiana* (Miller) K. Koch. Under the dense shade of the late summer canopy few competing herbs were present. I observed widely scattered plants of *Corallorhiza maculata* Rafinesque, *Maianthemum canadense* Desfontaines, *Monotropa uniflora* L., and *Epifagus virginiana* (L.) Barton. Most of the *Triphora* were restricted to leaf-lined depressions on gentle slopes.

Triphora's hemlock and beech habitat is regenerating in western Massachusetts and southern Vermont, and this tiny orchid is likely to be found at several new stations if a search is made for it. The four sites I visited are on private land, and are threatened by road widening, logging, or development.

My sincere thanks to Roberta Poland and Herman Willey for generously sharing their knowledge of Vermont orchids with me, and to Bruce Sorrie for providing the Massachusetts herbarium records. Funding for field work was supplied by the Pringle Herbarium, the Vermont chapter of The Nature Conservancy, and a grant from the Andrew Mellon Foundation.

LITERATURE CITED

Coddington, J. & K. G. Field. 1978. Rare and Endangered Vascular Plant Species in Massachusetts. The New England Botanical Club in cooperation with the U.S. Fish & Wildlife Service, Newton Corner, MA. 52 pp.

Countryman, W. D. 1978. Rare and Endangered Vascular Plant Species in Vermont. The New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service, Newton Corner, MA. 68 pp.

Crow, G. E., W. D. Countryman, G. L. Church, L. M. Eastman, C. B. Hellquist, L. L. Mehrhoff, & I. M. Storks. 1981. Rare and endangered vascular plant species in New England. Rhodora **83**: 259–299.

Rugg, H. G. 1950. Rare orchids in Vermont. Joint Bulletin of the Vermont Botanical and Bird Clubs **18**: 51–55.

PRINGLE HERBARIUM
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LITERATURE FOR NEW ENGLAND BOTANISTS

HELLQUIST, C. B. & G. E. CROW. 1980. Aquatic Vascular Plants of New England: Part 1. Zosteraceae, Potamogetonaceae, Zannichelliaceae, Najadaceae. New Hampshire Agricultural Experiment Station Bulletin **515.** Durham, N.H. 03824.

CROW, G. E. & C. B. HELLQUIST. 1981. Aquatic Vascular Plants of New England: Part 2. Typhaceae and Sparganiaceae. New Hampshire Agricultural Experiment Station Bulletin **517.** Durham, N.H. 03824.

HELLQUIST, C. B. & G. E. CROW. 1981. Aquatic Vascular Plants of New England: Part 3. Alismataceae. New Hampshire Agricultural Experiment Station Bulletin **518.** Durham, N.H. 03824.

CROW, G. E. & C. B. HELLQUIST. 1982. Aquatic Vascular Plants of New England: Part 4. Juncaginaceae, Scheuchzeriaceae, Butomaceae, Hydrocharitaceae. New Hampshire Agricultural Experiment Station Bulletin **520.** Durham, N.H. 03824.

HELLQUIST, C. B. & G. E. CROW. 1982. Aquatic Vascular Plants of New England: Part 5. Araceae, Lemnaceae, Xyricaceae, Eriocaulaceae, and Pontederiaceae. New Hampshire Agricultural Experiment Station Bulletin **523.** Durham, N.H. 03824.

This is a continuing series of reports on the aquatic and wetland plants of New England. There are technical keys to the species; habitat information, alkalinity and pH values and ranges. Detailed line drawings, and dot distribution maps for each species are valuable features of the series.

MARY M. WALKER
LIBRARIAN
NEW ENGLAND WILD FLOWER SOCIETY
FRAMINGHAM, MA 01701

NOTICES OF PUBLICATION

BATSON, WADE T. 1982. *Genera of the Western Plants.* 207 pp. Wade T. Batson, 1120 Blake Drive, Cayce, S.C. 29033. (Price $8.50)

The author provides dichotomous keys to the 1669 genera of western plants in this compact guide. The unique feature of the keys is that they are illustrated with line drawings showing important diagnostic features of each genus. Only the small size of drawings detracts from the usefulness of this feature. Of more interest to *Rhodora* readers may be the author's earlier book: BATSON, WADE T. 1977. *Genera of the Eastern Plants.* John Wiley, New York, N.Y. (Price $6.95)

SEYMOUR, FRANK CONKLING. 1982. *The Flora of New England.* 2nd. ed. xvii + 611 pp. Phytologia Memoirs **V,** H. N. Moldenke, 303 Parkside Rd., Plainfield, NJ, 07060. (Available from the author, Frank C. Seymour, 264 Hixville Rd., N. Dartmouth, MA, 02747 for $21.32, includes postage.

New England botanists especially will welcome the fact that *The Flora of New England,* for sometime out of print, is again available. The second edition contains line drawings by Andrea Robbins, instead of photographs, and there are seven pages of additions and corrections.

Vol. 84, No. 840, including pages 453 -559, was issued November 26, 1982.

Joint Meeting: June 20, 21, & 22, 1983

The annual joint Field Meeting of
The Northeastern Section of the Botanical Society of America,
The Torrey Botanical Club, and
The Philadelphia Botanical Club
will be held at Aurora, New York, with Cornell University and Wells College as host organizations. There will be accommodations at Wells College; primary field leadership will be supplied by Cornell University.

Tentative plans include: half-day trips to Great Gully, Zurich Mud Pond, Clark's Reservation, Oneida Lake, Cornell Plantations, Taughannock Gorge, etc. Some possible optional trips for the 23rd include Geneva Experiment Station, an illustration of old-field succession, Sapsucker Woods Bird Sanctuary, and a local winery.

Full details will be available after 1 February 1983 by writing the chairman:

Dr. Charles Burch
Wells College
Aurora, NY 13026 (Telephone: 315 364-7726)

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JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

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Cover illustration

Trollius laxus Salisb. is very rare as it nears its northeastern limit in Connecticut. Some old records indicate that it has grown in parts of New Hampshire and Maine, so it may yet be found in appropriate habitat.

Original artwork by Tess Feltes, Illustrator.

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NEW ENGLAND BOTANICAL CLUB

Vol. 85 April 1983 No. 842

THE GENUS *ENCYCLIA* HOOK. (ORCHIDACEAE) IN THE BAHAMA ARCHIPELAGO

RUBEN P. SAULEDA AND RALPH M. ADAMS

The neotropical genus *Encyclia* is represented by 13 species, 2 varieties, and 2 natural hybrids in the Bahama Islands, including the Turks and Caicos Islands. As such, it is the largest orchid genus, comprising more than 27 percent of all the orchid species distributed in the Bahama archipelago. For a complete inventory of the 52 orchid taxa that occur in the Bahama Archipelago, see Correll and Correll (1982). Of the 17 taxa of *Encyclia* in the Bahama archipelago, 7 are endemic, 3 share distributions only with Florida, 3 share distributions only with Cuba, and 1 shares its distribution only with Hispaniola. The remaining 3 taxa are more widely distributed (Table I).

Adams, et al., (1982) described 9 distinct and recognizable habitats that occur on the islands of the Bahama Archipelago. Species of the genus *Encyclia* occur in all of these habitats except pine forests and saltwater marsh and tidal flats. While the majority of the taxa in the genus occupy several habitats, a definite habitat preference exists, with all 17 taxa occurring either in high coppices, low coastal coppices, or both (Table II).

This paper represents the first modern and comprehensive taxonomic and ecological treatment of the genus in the archipelago.

For the purposes of this floristic study, we have chosen to use the broader generic concept as proposed by Dressler (1961). This concept differs from the original concept of *Encyclia* as proposed by Hooker (1828) and later expanded by Schlechter (1915). The

Dressler (1961) concept of *Encyclia* includes two species, *Encyclia boothiana* (Lindl.) Dressler and *Encyclia cochleata* (L.) Lemee, that do not correspond to the Hooker (1828) and Schlechter (1915) generic concept.

TAXONOMIC TREATMENT

Encyclia Hook., Bot. Mag. **55**: t2831. 1828.

Epiphytic or epilithic, rhizomatous plants. Stem pseudobulbous having one to many leaves at apex. Leaves entire, thinly coriaceous to rigid or semi-terete, slender and elongated. Inflorescence terminal, a simple raceme or panicle, often with an elongated peduncle, occasionally originating within a slender, conduplicate, foliaceous sheath. Flowers showy or inconspicuous, variously arranged, often non-resupinate. Sepals and petals free, spreading, or reflexed. Labellum free or variously adnate to column, entire or 3-lobed, disc variously callose. Column fleshy, without basal foot, cylindric, occasionally apically 3-to 5-dentate, commonly with auricles. Anther terminal, operculate, incumbent, 2-celled. Pollinia 4 (8 in triandrous varieties), equal, compressed, waxy, connected by a viscidium, without a stipe or gland. Stigmata 2, confluent, transverse. Capsule ovoid to ellipsoid, with prominent ribs or broadly 3-winged.

Type: **Encyclia viridiflora** Hook.

KEY TO SPECIES IN THE BAHAMA ARCHIPELAGO

1. Inflorescence basally enclosed by scarious slender conduplicate foliaceous sheath 2
2. Flowers resupinate 3
3. Column with one anther . . . 1. *E. boothiana* var. *boothiana*
3a. Column with three anthers . . . . . 2. *E. boothiana* var. *erythronioides*
2a. Flowers non-resupinate 4
4. Column with one anther . . . . 4. *E. cochleata* var. *cochleata*
4a. Column with three anthers . . . . . 5. *E. cochleata* var. *triandra*

1a. Inflorescence with basal foliaceous sheath absent 5

Table I. The distribution of the species of *Encyclia* within and between islands of the Bahama Archipelago. The islands are listed, from left to right, by decreasing area. The abbreviations are: C, Cuba; CA, Central America and, or Mexico; F, Florida; H, Hispaniola; J, Jamaica; SA, South America

	Andros	Great & Little Abaco	Great Inagua	Grand Bahama	Eleuthera	Acklin's Island	Long Island	Cat Island	Grand Caicos	Mayaguana	Crooked Island	North Caicos	New Providence	Great Exuma	San Salvador	Providenciales	Little Inagua	Rum Cay	Great Harbor Cay	Little Exuma	South Caicos	North Bimini	Frazer's Hog Cay	South Bimini	Norman's Cay	Staniard Cay	Additional Distributions
Encyclia boothiana var. boothiana	•																										C, H, CA
Encyclia boothiana var. erythronioides	•	•																									F
Encyclia caicensis												•									•						Endemic
Encyclia cochleata var. cochleata	•	•		•									•														C, H, J, CA, SA
Encyclia cochleata var. triandra	•																										F
Encyclia fehlingii	•	•		•									•									•	•	•			Endemic
Encyclia fucata	•	•		•																				•			C
Encyclia gracilis	•	•	•	•	•			•	•		•		•	•							•					•	Endemic
Encyclia hodgeana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			•					•	•	H
Encyclia inaguensis									•			•				•	•											Endemic
Encyclia plicata	•	•											•															C
Encyclia rufa	•	•	•	•	•		•	•	•		•	•	•	•	•	•	•		•	•		•	•	•				C
Encyclia selligera	•																											CA
Encyclia tampensis	•	•																										F
Encyclia withneri	•																											Endemic
Encyclia x bajamarensis	•	•																										Endemic
Encyclia x lucayana	•	•																										Endemic

5. Leaves non-deciduous, abscission layer at leaf base absent 6
6. Labellum yellow with radiating purple lines; flowers May to July . . . . . 16. *E. ×bajamarensis*
6a. Labellum white with radiating purple lines; flowers July through September 7
7. Labellum to 2.7 cm long, 2.8 cm wide; callosity on labellum under column is two lateral erect keels merging into a single keel at junction of lobes and extending into disc . . . . . 8. *E. gracilis*
7a. Labellum to 1.9 cm long, 1.9 cm wide; callosity on labellum under column is two lateral erect keels joined by a third keel at junction of lobes and all three keels extending into disc . . . . . 17. *E. ×lucayana*
5a. Leaves normally deciduous 8
8. Pseudobulbs elliptic to ovate 9
9. Labellum recurved or reflexed 10
10. Auricles at apex of column pointed and incurved; disc of labellum with two fleshy pads and strongly pleated; callosity under column terminating in two fleshy tubercles . . . . . 11. *E. plicata*
10a. Auricles short, square; disc of labellum without fleshy pads and without pleats; lateral margins of disc revolute . . . . . 12. *E. rufa*
9a. Labellum not recurved 11
11. Auricles absent 12
12. Labellum purple . . . . . 13. *E. selligera*
12a. Labellum white or yellowish-white with purple spots or lines . . . . . 7. *E. fucata*
11a. Auricles present at apex of column 13
13. Pedicel muricate . . . . . 15. *E. withneri*
13a. Pedicel glabrous 14
14. Callosity on labellum under column distally terminating abruptly in a fleshy 3-dentate plate . . . . . 6. *E. fehlingii*
14a. Callosity on labellum under column not terminating abruptly . . . . . 14. *E. tampensis*
8a. Pseudobulbs linear-lanceolate, narrowly attenuate toward apex 15

15. Lateral margins of disc of labellum revolute .....
..... 10. *E. inaguensis*
15a. Lateral margins not revolute 16
16. Flowers ascending and closely spaced on short, erect lateral branches ..... 3. *E. caicensis*
16a. Flowers not ascending or closely spaced, lateral branches not erect ..... 9. *E. hodgeana*

1. **Encyclia boothiana** (Lindl.) Dressler, Brittonia **13**:269, 1961, var. **boothiana** (Fig. 1).
Basionym: *Epidendrum boothianum* Lindl., Bot. reg. 24:Misc. 5. 1838. HOLOTYPE: Sutton s.n., Cuba (K-L, photograph seen[1]).

Plant epiphytic, rhizomatous, to 26 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping, completely enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, suborbicular to ovate, strongly flattened, to 6 cm long, 6 cm wide, 15 mm thick, basally enclosed by fugacious scarious sheaths, to 3-leaved at apex; leaves thinly coriaceous, keeled, oblong to oblanceolate, obtuse to acute, apex recurved, to 15 cm long, 2.0 cm wide; inflorescence terminal, to 20 cm tall; peduncle slender, loosely racemose above, basally enclosed by a scarious, slender, linear-oblong, conduplicate, foliaceous sheath; raceme loosely few-flowered, to 15-flowered; floral bracts minute, subulate, acute, concave, membranaceous, to 3 mm long, 2 mm wide; ovary pedicellate, slender, to 17 mm long; sepals green with purplish-brown irregular blotches, glossy, rigid, oblanceolate, acute to subacuminate, margins slightly revolute, to 15 mm long, 4 mm wide; petals green with purplish-brown irregular blotches, glossy, rigid, narrowly oblanceolate, obtuse to acute, to 14 mm long, 4 mm wide; labellum basally adnate to column, entire or obscurely 3-lobed, to 14 mm long, 6 mm wide, rhombic or trapeziform in outline, white to greenish white, all lobes obtuse, lateral lobes reflexed, callosity on disc white, edged with purple, tridentate, middle tooth thickened extending to apex of disc; column to 8 mm long, 6 mm wide, white, greenish at base, with purple blotches, each side strongly longitudinally grooved, apex of

[1]All specimens cited in this paper have been examined, unless otherwise noted.

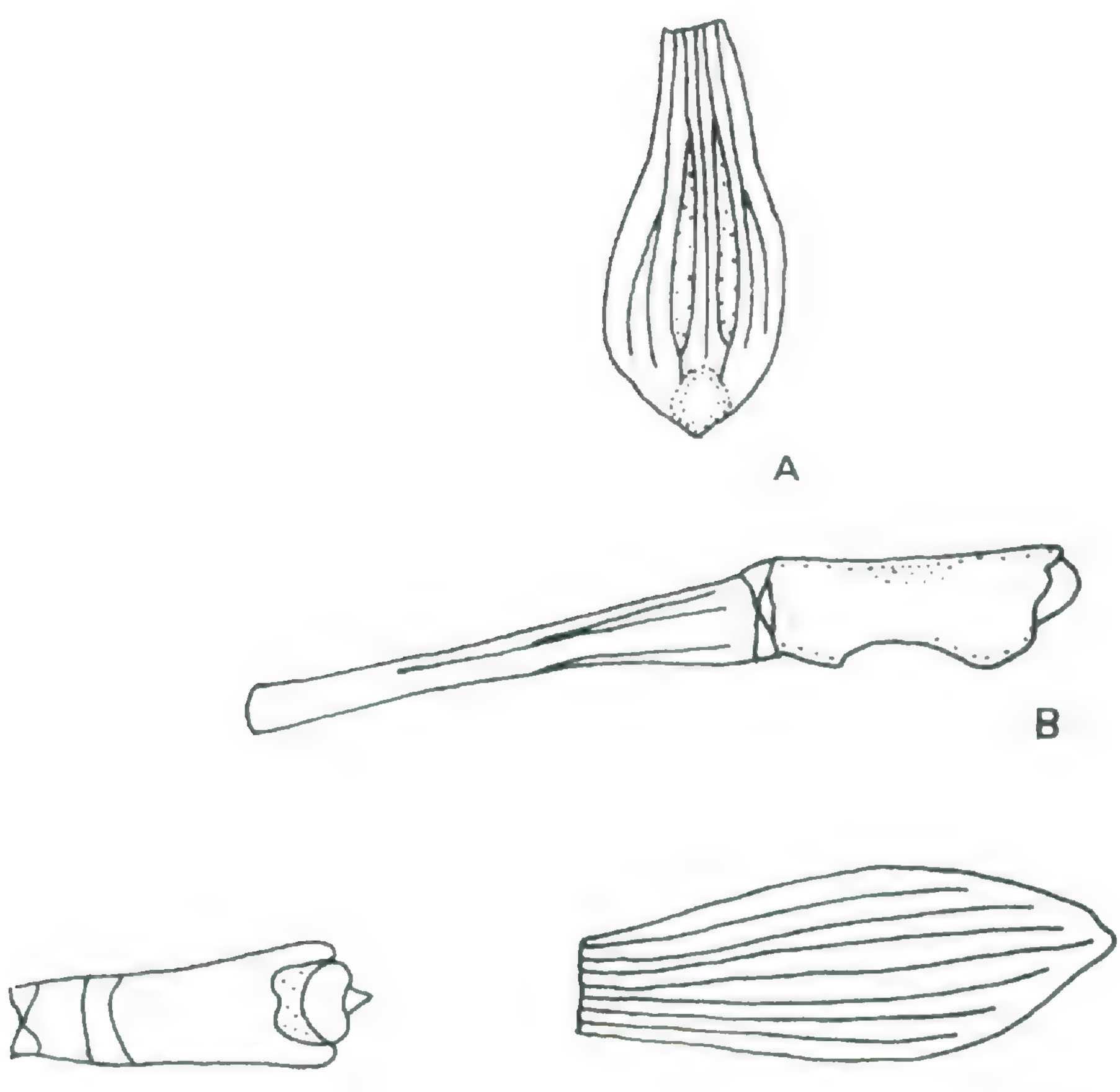


Figure 1. *Encyclia boothiana* (Lindl.) Dressler var. *boothiana*. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. lateral sepal; **F**. Petal.

Table II. The species of *Encyclia* in the Bahama Archipelago and the habitats within which they occur.

	Beach & Dune	Coastal Rock Scrub	Low Coastal Coppice	High Coppice	Inland Scrub	Pine Forest	Freshwater Marsh & Swamp	Saltwater Marsh & Tidal Flats	Mangrove Forest	Disturbed Areas
Encyclia boothiana var. boothiana				•						
Encyclia boothiana var. erythronioides				•					•	
Encyclia caicensis	•	•	•							
Encyclia cochleata var. cochleata				•						
Encyclia cochleata var. triandra				•						
Encyclia fehlingii			•	•					•	
Encyclia fucata			•	•			•		•	
Encyclia gracilis	•	•	•		•					•
Encyclia hodgeana		•	•	•	•					
Encyclia inaguensis		•	•							
Encyclia plicata			•	•					•	
Encyclia rufa	•	•	•	•	•					
Encyclia selligera			•							
Encyclia tampensis			•							
Encyclia withneri				•						
Encyclia x bajamarensis			•							
Encyclia x lucayana			•							•
Total Number of Taxa	3	5	12	10	3	0	1	0	4	2

column 3-toothed, anther yellow, pollinia 4; capsule pendent, 3-winged, to 1.5 cm long, 1.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Andros**, high coppice, 6 mi NW of Love Hill settlement, 10 July 1976, *Sauleda 1882* (FAU).

ADDITIONAL DISTRIBUTION: **Cuba,** *Hioram 2117* (NY); Isle of Pines, Cuba, *Taylor 78* (NY); **Haiti,** *Leonard and Leonard 13381* (NY); **Mexico,** *Nagel 4967* (US); **British Honduras,** *Gentle 1146* (NY).

REPRODUCTIVE PERIOD: May through October.

ECOLOGY: This rare species is found growing epiphytically on *Lysiloma latisiliqua* (L.) Benth., and is found in High Coppices.

ADDITIONAL COMMENTS: This species does not properly belong in the genus *Encyclia* Hook.. However, in the absence of a comprehensive monographic treatment which unequivocally establishes its true generic position, we have chosen to include it here.

2. **Encyclia boothiana** (Lindl.) Dressler var. **erythronioides** (Small) Luer, Florida Orchidist, **14**: 29. 1971 (Fig. 2).

Basionym: *Epidendrum erythronioides* Small, Fl. Southeastern U.S., 328. 1903.

Epicladium boothianum (Lindl.) Small var. *erythronioides* (Small) Acuna, Cat. Descr. Orq. Cub **60**: 89. 1938. HOLOTYPE: Key Largo, Florida, *Curtis s.n.* (NY).

Plant epiphytic or epilithic, rhizomatous, to 23 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping, completely enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, suborbicular to ovate, strongly flattened, to 5 cm long, 4 cm wide, 1.5 cm thick, basally enclosed by fugacious scarious sheaths, to 3-leaved at apex; leaves thinly coriaceous, keeled, oblong to oblanceolate, obtuse to acute, apex reflexed, to 12 cm long, 1.5 cm wide; inflorescence terminal, to 18 cm tall, peduncle slender, loosely racemose above, basally enclosed by a scarious, slender, linear-oblong, conduplicate foliaceous sheath, raceme loosely few-flowered, to 8-flowered; floral bracts minute, membranaceous, subulate, acute, concave, to 3 mm long, 2 mm wide; ovary pedicellate, slender, to 17 cm long; sepals green with purplish-brown irregular blotches, glossy, rigid, oblanceolate, acute to subacuminate, margins slightly revolute, to 14 mm long, 3 mm wide; petals green with purplish-brown irregular blotches, glossy, rigid, narrowly oblanceolate,

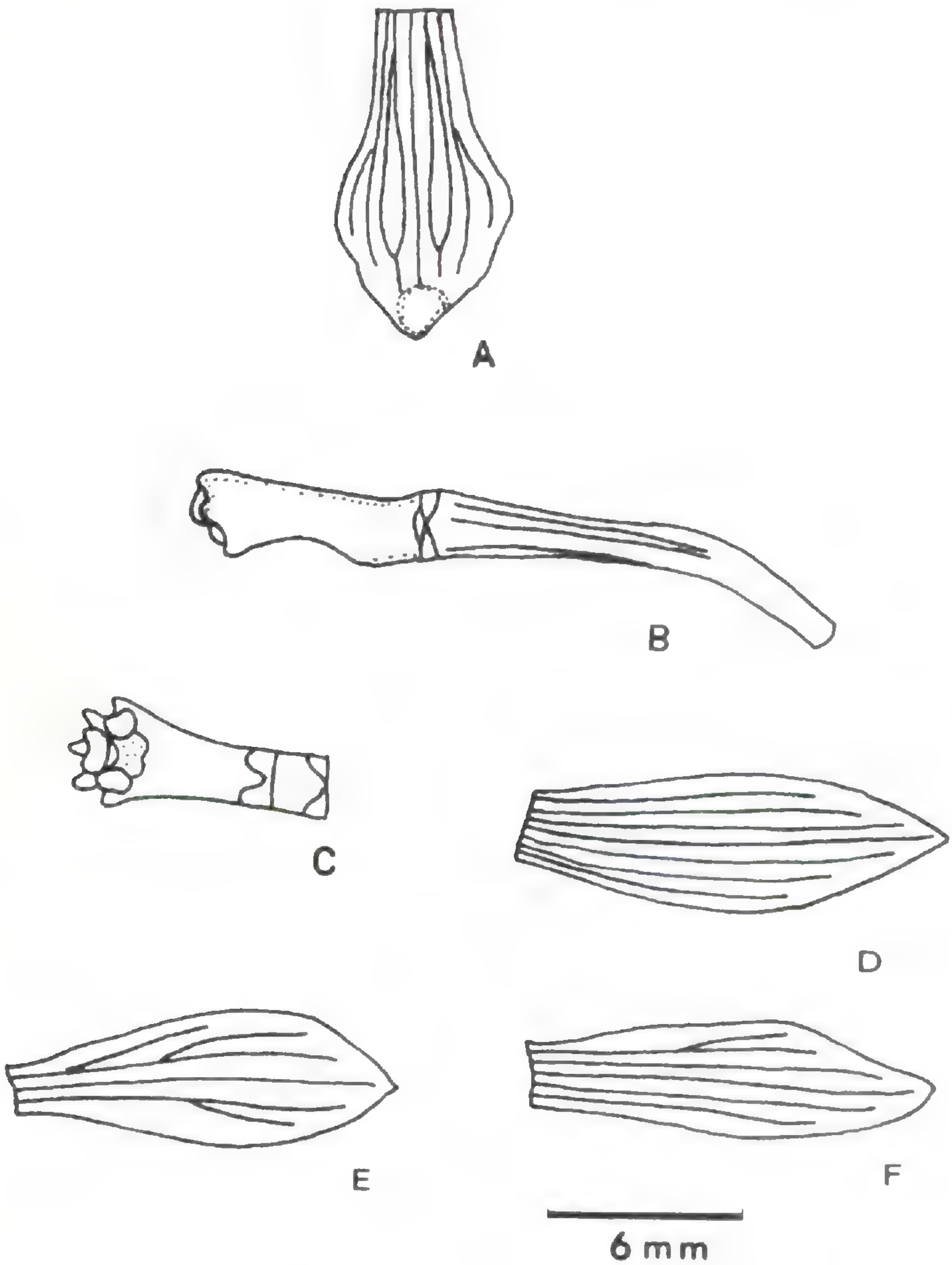


Figure 2. *Encyclia boothiana* (Lindl.) Dressler var. *erythronioides* (Small) Luer. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

obtuse to acute, to 13 mm long, 3 mm wide; labellum basally adnate to column, entire or obscurely 3-lobed, rhombic or trapeziform in outline, white to greenish-white, to 12 mm long, 5 mm wide, all lobes obtuse, lateral lobes recurved, callosity on disc white, edged with purple, tridentate, middle tooth thickened, extending to apex of disc; column to 8 mm long, 6 mm wide, white, greenish at base, with purple blotches, each side strongly longitudinally grooved, apex of column 5-toothed, with 3 yellow anthers, central anther with 4 pollinia, 2 lateral anthers with 2 pollinia each; capsule pendent, 3-winged, to 1.5 cm long, 1.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Andros,** high coppice, 3 mi NW of Love Hill settlement, 10 July 1976, *Sauleda 1102* (M), *1104* (FTG), *1105* (NY), *1106* (F), *1107* (US), *1108* (SEL), *1109* (P), *1110* (AMES), *1111* (K), *1113* (F); mangrove along lake shore, 1 mi NW of Love Hill settlement, 16 April 1977, *Sauleda 1865* (FAU); Deep Creek, 18 Aug.–10 Sept. 1906, *Brace 5133* (F, NY).

ADDITIONAL DISTRIBUTION: **Florida,** *Curtis s.n.* (NY).

REPRODUCTIVE PERIOD: May through September.

ECOLOGY: This variety is found growing epiphytically on *Lysiloma latisiliqua* (L.) Benth., *Coccoloba diversifolia* Jacq., *Rhizophora mangle* L. and *Conocarpus erectus* L. The habitats in which it is found are High Coppice and Mangrove Forest. This triandrous variety is the most common variety found in the Bahama Islands and is usually autogamous and occasionally cleistogamous.

3. **Encyclia caicensis** Sauleda and Adams, Selbyana **2** (4): 340. 1978 (Fig. 3).

TYPE: South Caicos, 200 m SE of airport runway, large clump growing epiphytically on *Pithecellobium bahamense* Northrop, 11 Feb. 1978, in flower, *Sauleda, Adams, Adams, and Correll 2031* (HOLOTYPE: NY; ISOTYPES: AMES, K, SEL, US, USF).

Plant epiphytic or rarely epilithic, rhizomatous, to 260 cm tall; roots numerous, slender to thick, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by scarious imbricating sheaths; secondary stems modified into pseudobulbs, erect, clustered, distinctly elongated, attenuate, linear-lanceolate, to 15 cm long, 5 cm thick, enclosed by scarious imbricating sheaths, to 4-leaved at apex; leaves coriaceous to rigid, erect, linear to linear-lanceolate, acute, to 60 cm long, 3.0 cm wide; inflorescence terminal,

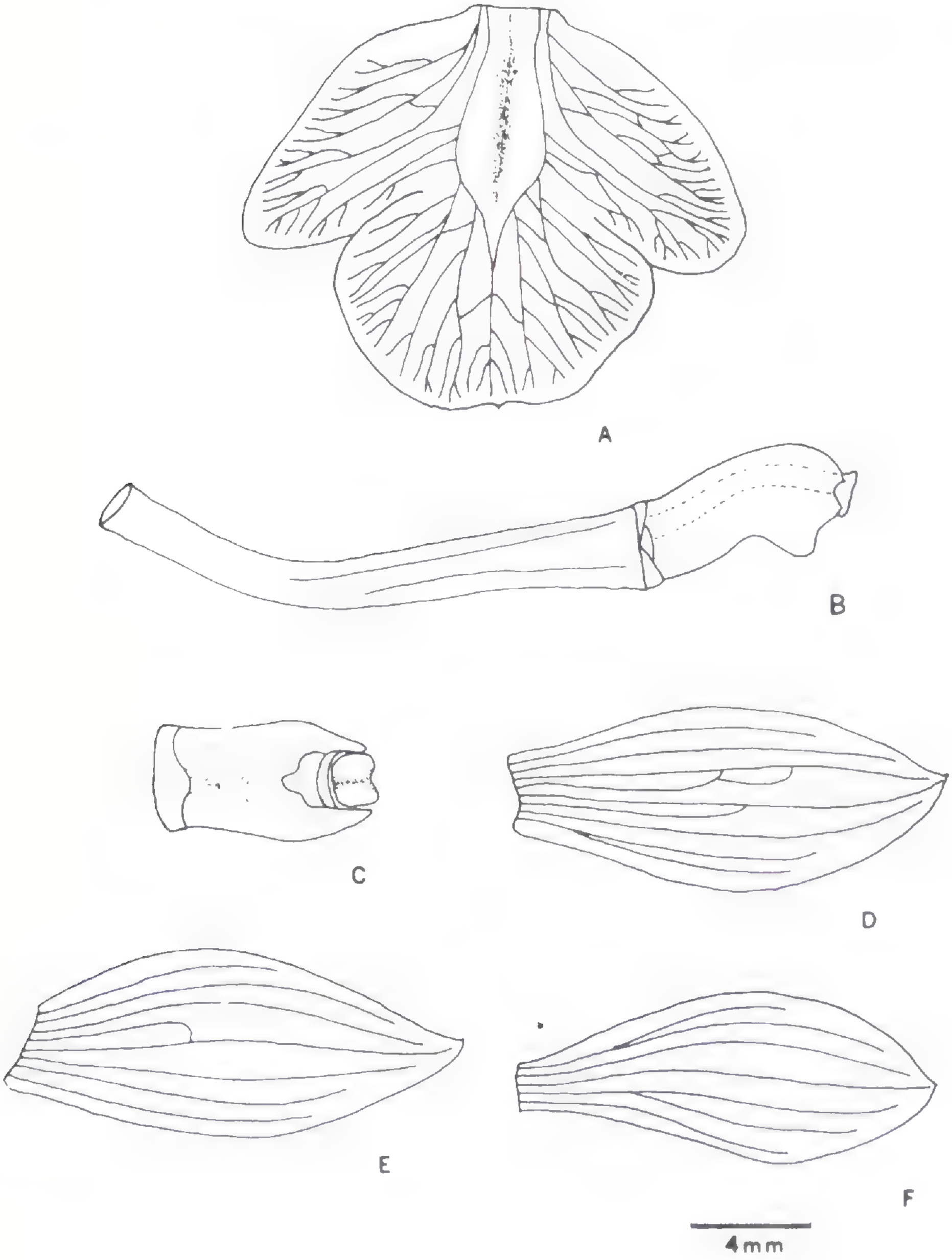


Figure 3. *Encyclia caicensis* Sauleda and Adams. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

to 215 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, lateral branches stiff and erect, to 60 ascending flowers; floral bracts broadly ovate-triangular, acute, to 3.0 mm long, 4.0 mm wide; ovary pedicellate, slender, to 2.8 cm long; sepals greenish-yellow to tan suffused and/or striped with reddish-brown, elliptical, acute, to 1.8 cm long, 7.0 cm wide; petals greenish-yellow to tan with reddish-brown suffusion or striping, obovate, acute, to 1.6 cm long, 5.0 mm wide; labellum free, 3-lobed, to 1.9 cm long, 1.9 cm wide, white to yellowish-white with radiating reddish-purple stripes, lateral lobes yellow, orbicular to ovoid, obtuse, erect, embracing column, midlobe with yellowish margin, orbicular, apically recurved, callus distinctly white with reddish-purple stripes, composed of two erect, decurrent lateral keels uniting at midlobe; column short, blunt, to 8.0 mm long, 5.0 mm wide, white to greenish-white, streaked with purple, with membraneous, incurved, rounded auricles, anther cap yellow; capsule pendent, to 2.8 cm long, 2.1 cm thick.

DISTRIBUTION IN THE TURKS AND CAICOS ISLANDS: **South Caicos**, SE of runway, epiphytic, 11 Feb. 1978, *Sauleda, Adams, Adams, and Correll 2026* (FTG), *2027* (P), *2028* (LE), *2029* (F), *2030* (S). **Middle Caicos**, Moujean Harbor, on top of ridge, 11 Feb. 1978, *Sauleda, Adams, and Correll 2045* (FAU). **North Caicos,** Horse Stable, epiphytic, 12 Feb. 1978, *Sauleda, Adams, Adams and Correll 2046* (BM); Whitby's Landing and vicinity, 28 Feb.–2 March 1911, *Millspaugh and Millspaugh 9168* (F); between Bottle Creek and Whitby, epiphytic on palms, near beach, 24 April 1954, *Lewis s.n.* (AMES). **Ambergris Cay**, 12 March 1911, *Millspaugh and Millspaugh 9299, 9304* (F, NY). **Little Ambergris Cay**, 13 March 1911, *Millspaugh and Millspaugh 9319* (F, NY). **Dellis' Cay**, 4 March 1911, *Dellis 1* (F).

REPRODUCTIVE PERIOD: January through April.

ECOLOGY: On islands in the Caicos Group this heliophilic species is abundant, growing epiphytically on *Pithecellobium bahamense* Northrop, *Pithecellobium guadalupense* (Pers.) Chapm., *Coccoloba tenuifolia* L., *Coccoloba uvifera* (L.) Jacq. and *Coccothrinax argentata* (Jacq.) L.H. Bailey and rarely epilithically on Pleistocene limestone. The habitats in which it is found are Beach and Dune, Coastal Rock Scrub, and Low Coastal Coppice. Endemic.

ADDITIONAL COMMENTS: Specimens of this species were first collected on the Caicos Islands in 1911 by Millspaugh and Millspaugh and were incorrectly identified as *Epidendrum diurnum* (Jacq.) Cogniaux, an epithet subsequently transferred to *Encyclia diurna*

(Jacq.) Britton and Millspaugh and applicable to a South American species which is distinct from this species.

Encyclia caicensis is similar to and may be confused with *Encyclia hodgeana* (Hawkes) Beckner and non-reproductive plants of *Encyclia inaguensis* (Nash) Britton and Millspaugh.

Encyclia caicensis differs from *E. hodgeana* vegetatively, by having narrower and more rigid and erect leaves. Florally, these two species differ significantly. The inflorescence of *E. caicensis* has shorter and more numerous lateral branches which are distinct in their ascending habit. The flowers are smaller, more numerous and more tightly clustered than in *E. hodgeana*. The cupped shape and ascending habit of the flowers of *E. caicensis* further separate it from it sympatric congener, *E. hodgeana*. Furthermore, the labellum is not as deeply three-lobed, the labellum apex (disc) distinctly more recurved, and the column disproportionately shorter in *E. caicensis* than in *E. hodgeana*.

Encyclia inaguensis has distinctly narrower leaves than immature and small specimens of *E. caicensis* (and *E. hodgeana*) with which it might be confused. All three species have large sympatric populations occurring on the Caicos Islands.

4. **Encyclia cochleata** (L.) Lemee, Fl. Guyane Francaise I: 418, 1955, var. **cochleata** (Fig. 4).

Basionym: *Epidendrum cochleatum* L. Sp. Pl., ed. 2, 2:1351. 1763.

Anacheilium cochleatum (L.) Hoffmsg., Verz. Orch. 21. 1842. HOLOTYPE: Boerhaave's copy, made by Claude Aubriet, of the Plumier plate, reproduced by Burman in Plantarum Americanarum Fasciculus (1758, p. 180, t.185, f. 2) and now at the University Library at Groningen, Netherlands.

Plant epiphytic or epilithic, rhizomatous, to 50 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, elliptic to ovate, stipitate below, strongly compressed, to 15 cm long, 5 cm wide, basally enclosed by fugacious scarious sheaths, to 3-leaved at apex; leaves thinly coriaceous, elliptic to lanceolate, acute, to 24 cm long, 4 cm wide; inflorescence terminal, to 35 cm tall, flowers opening serially, peduncle slender, loosely racemose above, basally

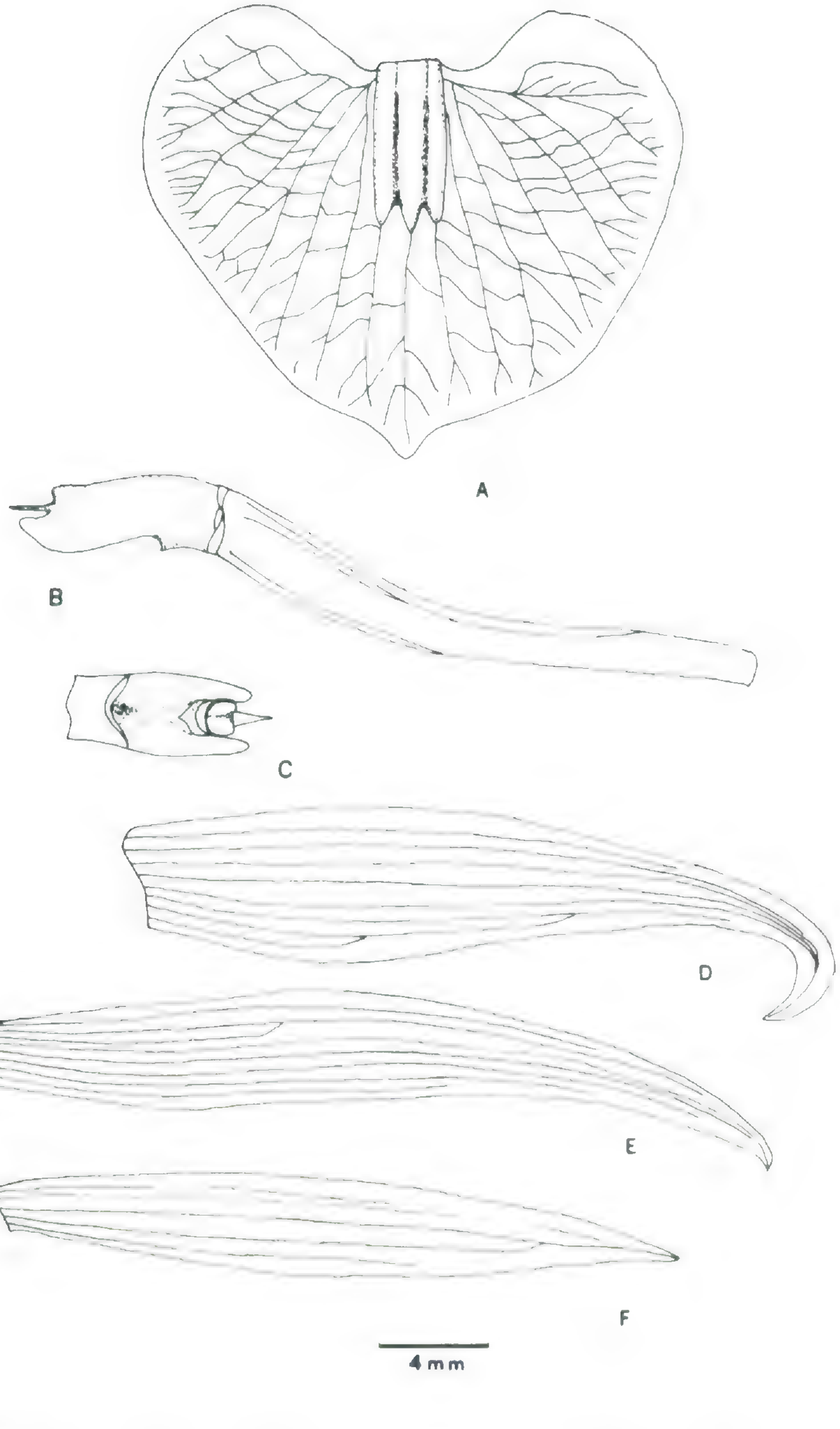


Figure 4. *Encyclia cochleata* (L.) Lemee var. *cochleata*. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

enclosed by a scarious, slender, linear-oblong, conduplicate, foliaceous sheath; raceme loosely few-flowered; to 15 non-resupinate flowers; floral bracts minute, triangular to lanceolate, acute to acuminate, concave, membranaceous, to 6 mm long, 4 mm wide; ovary pedicellate, slender, triquetrous, winged, to 3.5 cm long; sepals and petals green or greenish-yellow with purple blotches near the base, linear-lanceolate, subacuminate, twisted and reflexing inward, sepals to 4.5 cm long, 4 mm wide, petals to 3 cm long, 3 mm wide; labellum adnate to middle of column, entire, broadly orbicular to cordate, to 2 cm long, 2 cm wide, deep purple with basal portion greenish-white with radiating purple veins, disc with a yellow sulcate to ligulate callosity at base, margins undulate; column to 8 mm long, 4 mm wide, green with purple spots, erect, stout, apex 3-toothed, lateral teeth longer than mid-tooth, mid-tooth blunt and fleshy, single orange anther containing 4 pollinia; capsule pendent, 3-angled, broadly winged, to 4 cm long, 2.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** low coppice, Abaco Heights, 11 April 1979, *Sauleda and Correll 2283* (FAU). **Andros,** high coppice, 6 mi NW of Love Hill settlement, 10 May 1975, *Sauleda 1039* (AMES); Owens Town, high coppice, 8 May 1978, *Sauleda, Correll, Eckenwalder and Stevenson 2115* (FAU); Congo Town, 6 June 1975, *Sauleda 1054* (FAU); high coppice, 6 mi NW Love Hill settlement, 10 July 1976, *Sauleda 1100* (F), *1101* (K); coppice near Nicholl's Town, 4–5 Feb. 1905, *Small and Carter 8975* (NY). **New Providence**, Maiden Head Coppice, on trees, 24 Aug. 1904, *Britton and Brace 244* (F, NY). **Grand Bahama**, E of Coral Road, Freeport, 24 Jan. 1976, *Correll and Popenoe 46653* (FTG).

ADDITIONAL DISTRIBUTION: **Cuba,** *Shafer 13457* (NY); **Haiti,** *Nash 670* (NY); **Dominican Republic,** *Valeur 81* (NY); **Jamaica,** *Underwood 252* (NY); **Puerto Rico,** *Britton and Shafer s.n.* (NY); **Colombia,** *Smith 2859,* (NY); **Venezuela,** *Johnston 229* (NY).

REPRODUCTIVE PERIOD: Sporadically throughout year, mainly May through December.

ECOLOGY: This species grows mainly epiphytically on *Mastichodendron foetidissimum* (Jacq.) H.J. Lam. and *Calyptranthes pallens* (Poir.) Griesb. but is found occasionally growing epilithically. It is found in High Coppices.

ADDITIONAL COMMENTS: Pabst, et al. (1981) have reestablished the genus *Anacheilium* which includes this species as its type. While we agree that *Encyclia cochleata* probably more appropriately belongs in the genus *Anacheilium,* we have chosen to include it here,

since we have adopted the broader generic concept of Dressler (1961) for the purposes of this floristic study.

5. **Encyclia cochleata** (L.) Lemee var. **triandra** (Ames) Dressler, Brittonia **13**: 253. 1961 (Fig. 5).

Basionym: *Epidendrum cochleatum* L. var. *triandrum* Ames, Contr. Orchid. S. Fl. **16**, pl. 8. 1904.

Epidendrum triandrum (Ames) House, Muhlenbergia **1**: 129. 1906.

Anacheilium cochleatum var. *triandrum* (Ames) Small, Man. Southeast. Fl. 392. 1933. Holotype: Florida, *Eaton s.n.* (AMES).

Plant epiphytic or epilithic, rhizomatous, to 50 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, elliptic to ovate, stipitate below, strongly compressed, to 12 cm long, 4 cm wide, basally enclosed by fugacious scarious sheaths, to 3-leaved at apex; leaves thinly coriaceous, elliptic to lanceolate, acute, to 20 cm long, 4 cm wide; inflorescence terminal, to 38 cm tall, flowers opening serially, peduncle slender, loosely racemose above, basally enclosed by a scarious, slender, linear-oblong, conduplicate, foliaceous sheath; raceme loosely few-flowered, to 10 non-resupinate flowers; floral bracts minute, triangular to lanceolate, acute to acuminate, concave, membranaceous, to 10 mm long, 6 mm wide; ovary pedicellate, slender, triquetrous, winged, to 3 cm long; sepals and petals green or greenish-yellow with purple blotches near the base, linear-lanceolate, subacuminate, twisted and reflexing inward, sepals to 4 cm long, 3 mm wide, petals to 3 cm long, 3 mm wide; labellum adnate to middle of column, entire, broadly orbicular to cordate, to 2 cm long, 2 cm wide, deep purple with basal portion greenish-white with radiating purple veins, disc with a yellow sulcate to ligulate callosity at base, margins undulate; column to 8 mm long, 4 mm wide, green with purple spots, erect, stout, apex 5-toothed, anthers 3, orange, central anther containing 4 pollinia, 2 smaller lateral anthers containing 2 pollinia each; capsule pendent, strongly 3-angled, broadly winged, to 4 cm long, 2.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Andros,** high coppice, near Kemp's Bay, 8 Oct. 1976, *Sauleda 1131* (FAU), *1132* (FTG); coppice, Crow Hill, 25–27 January 1910, *Small and Carter 8738* (AMES, F, NY, US).

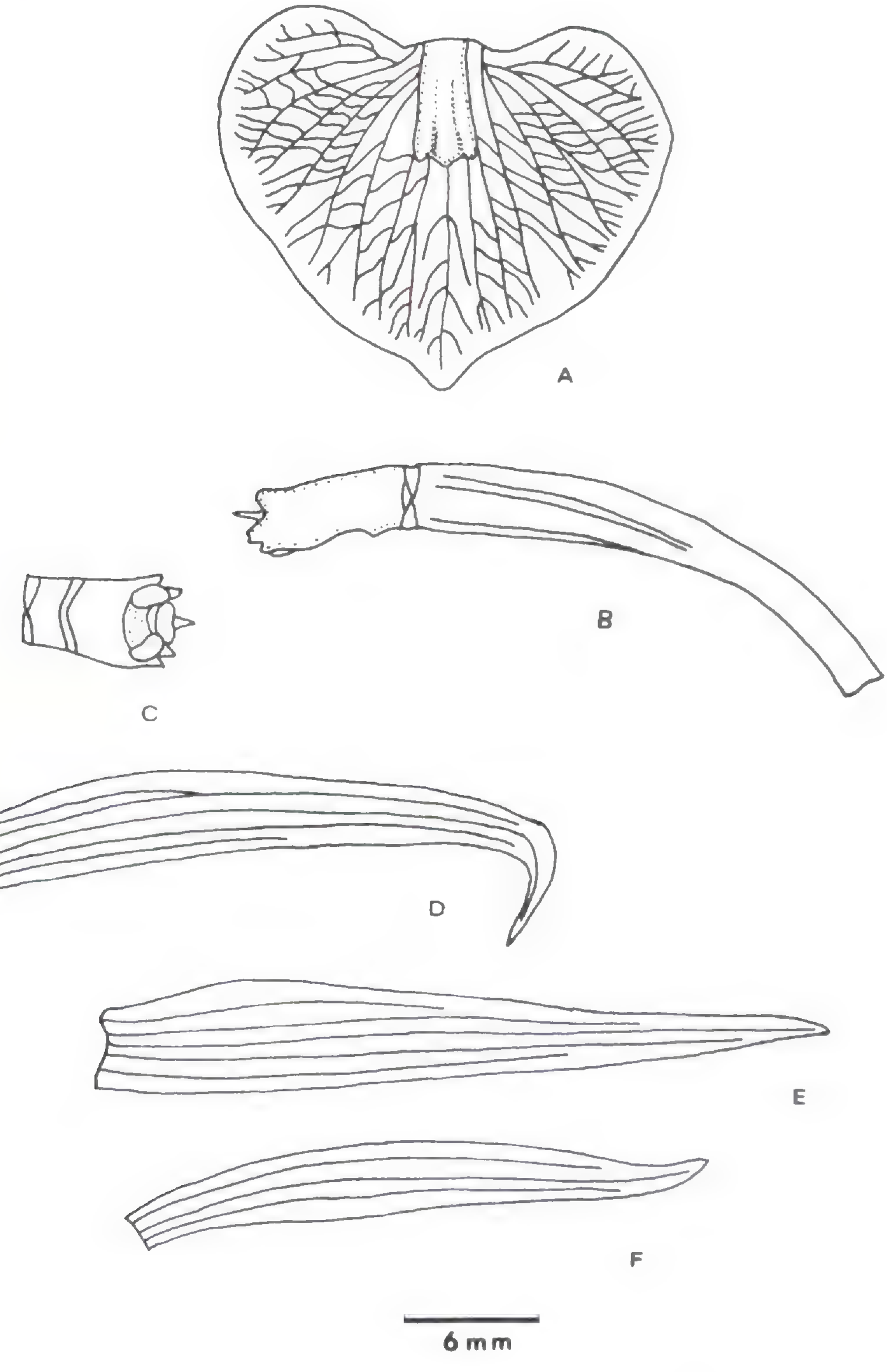


Figure 5. *Encyclia cochleata* (L.) Lemee var. *triandra* (Ames) Dressler. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

ADDITIONAL DISTRIBUTION: Florida, *Eaton s.n.* (AMES).

REPRODUCTIVE PERIOD: September through January.

ECOLOGY: This variety grows epiphytically on *Calyptranthes pallens* (Poir.) Griesb. and grows in High Coppices. Only one small population of this triandrous variety occurs in the Bahama Islands. All of the individuals examined in the population were triandrous and produced autogamous seed capsules. No triandrous individuals have been observed other than in this population.

6. **Encyclia fehlingii** (Sauleda) Sauleda and Adams, Brittonia **33**(2): 187. 1981 (Fig. 6).

Basionym: *Epidendrum fehlingii* Sauleda, Amer. Orchid Soc. Bull. **46**(1): 32–35. 1977. TYPE: Bahama Islands, Andros, *Sauleda 1028* (HOLOTYPE: AMES; ISOTYPES: FAU, NY, US, USF).

Encyclia tampensis auct. non (Lindl.) Small; Britton and Millspaugh, Bahama Fl. 91. 1920.

Encyclia acicularis auct. non (Batem.) Britton and Millspaugh; Britton and Millspaugh, Bahama Fl. 92. 1920.

Plant epiphytic or epilithic, rhizomatous, to 80 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, narrowly ovate, attenuate towards apex, to 9 cm long, 6 cm wide, basally enclosed by scarious sheaths, to 3-leaved at apex; leaves coriaceous to rigid, linear-oblong, acute, to 40 cm long, 3 cm wide; inflorescence terminal, to 71 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 50 flowers; floral bracts minute, ovate-triangular, obtuse, to 3 mm long, 3 mm wide; sepals green to greenish-yellow, rarely with brown striping toward apex, oblong to oblanceolate, acute, to 18 mm long, 5 mm wide; petals green to greenish-yellow, rarely with brown striping toward apex, obovate to oblanceolate, acute, to 17 mm long, 5 mm wide; labellum free, deeply 3-lobed, to 14 mm long, 18 mm wide, with parallel purple lines, lateral lobes narrowly triangular, obtuse, erect, midlobe rounded, emarginate, margin undulate, both sides revolute, disc at junction of lobes provided with a fleshy, plate-like callus, 3-dentate in front, lateral dents erect keels with an additional interrupted ridge on both sides, five radiating undulate lamellae in front of callus on

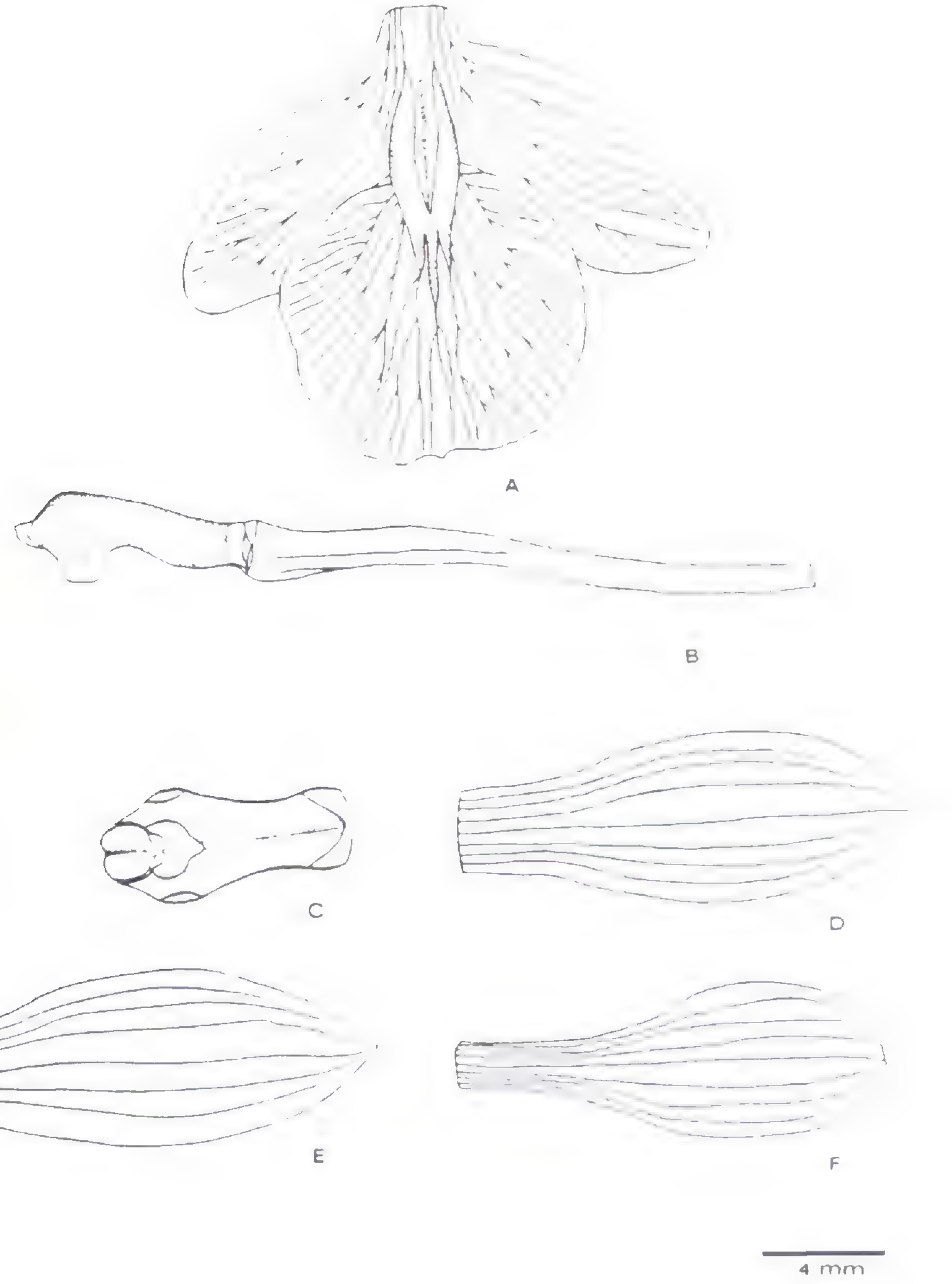


Figure 6. *Encyclia fehlingii* (Sauleda) Sauleda and Adams. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

midlobe; column white, to 10 mm long, 5 mm wide, elongate, slightly curved, with membraneous incurved rounded auricles, anther yellow; capsule pendent, to 3 cm long, 2 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** Abaco Heights, 11 April 1979, *Sauleda and Correll 2255* (FAU); Guiana Schooner Bay road, 12 April 1979, *Sauleda and Correll 2305* (FAU); Snake Cay road, 12 April 1979, *Sauleda and Correll 2313* (FAU); Boat Harbor Landing near Marsh Harbor, 6 July 1974, *Correll and Popenoe 42643* (FTG); coppice of Israel, 6 July 1974, *Correll, Popenoe and Patterson 42652* (FTG); near Sandy Point airport, 7 July 1974, *Correll and Popenoe 42706* (FTG). **Little Abaco,** low coppice, near Fox Cay settlement, 3 Aug. 1979, *Sauleda, Adams and Adams 2866* (FAU). **Andros,** Fresh Creek, on trees in coppice 1 mi NW of Love Hill settlement, 6 June 1975, *Sauleda 1025* (FTG), *1028* (AMES), *1045* (FAU); Mars Bay, 1 July 1890, *Northrop and Northrop 711* (NY); 3 mi S of Stafford Creek, 8 Oct. 1977, *Sauleda, 1982* (SEL), *1983* (NY), *1984* (K); Cedar Coppice, 7 May 1978, *Sauleda, Correll, Stevenson and Eckenwalder 2086* (FAU). **Berry Islands,** Chub Cay, low coppice, 1 mi E of airport, 21 April 1978, *Sauleda, Correll and Eckenwalder 2059* (FAU). **Grand Bahama,** coastal coppice, Golden Grove, 5–13 Feb. 1905, *Britton and Brace 2728* (NY, F). **New Providence,** Maiden Head Coppice, 24 Aug. 1904, *Britton and Brace 242* (AMES, F, NY); S of Fox Hills, 1904, *Britton and Brace 543* (NY). **Bimini Group,** South Bimini, 0.5 mi W of airport, 16 Feb. 1979, *Sauleda, Adams, Adams and Correll 2303* (FAU).

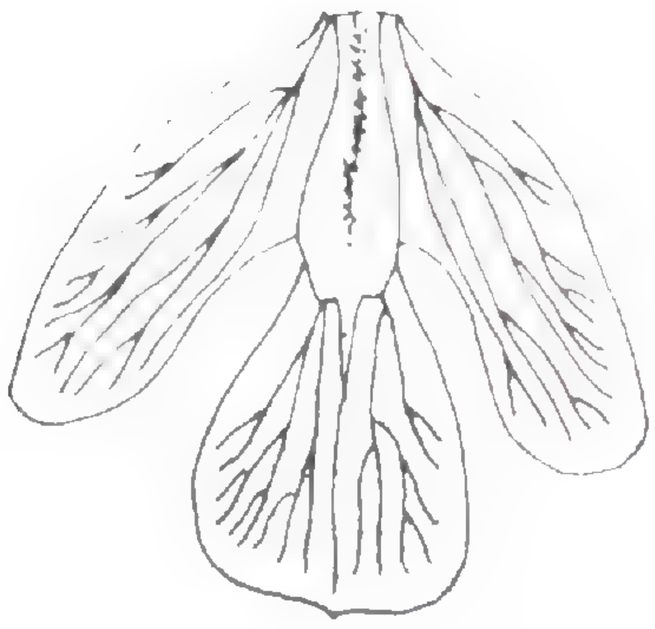
REPRODUCTIVE PERIOD: May through October.

ECOLOGY: This species grows epiphytically on *Rhizophora mangle* L., *Erythroxylum areolatum* L., *Conocarpus erectus* L., *Bucida spinosa* (Northrop) Jennings, *Acacia choriophylla* Benth., *Hypelate trifoliata* Sw., *Coccoloba diversifolia* Jacq., *Tabebuia bahamensis* (Northrop) Urban and *Psidium longipes* (Berg.) McVaugh. The habitats in which it occurs are Mangrove Forest, High Coppice and Low Coastal Coppice. Endemic.

7. **Encyclia fucata** (Lindl.) Britton and Millspaugh, Bahama Fl. 91. 1920 (Fig. 7).

   Basionym: *Epidendrum fucatum* Lindl., Bot. Reg. **24**: Misc. 15. 1838. HOLOTYPE: Cuba, *Sutton s.n.* (K–L, photograph seen).

Plant epiphytic or epilithic, rhizomatous, to 81 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, ovate, attenuate towards apex, to 6 cm long, 3 cm wide,



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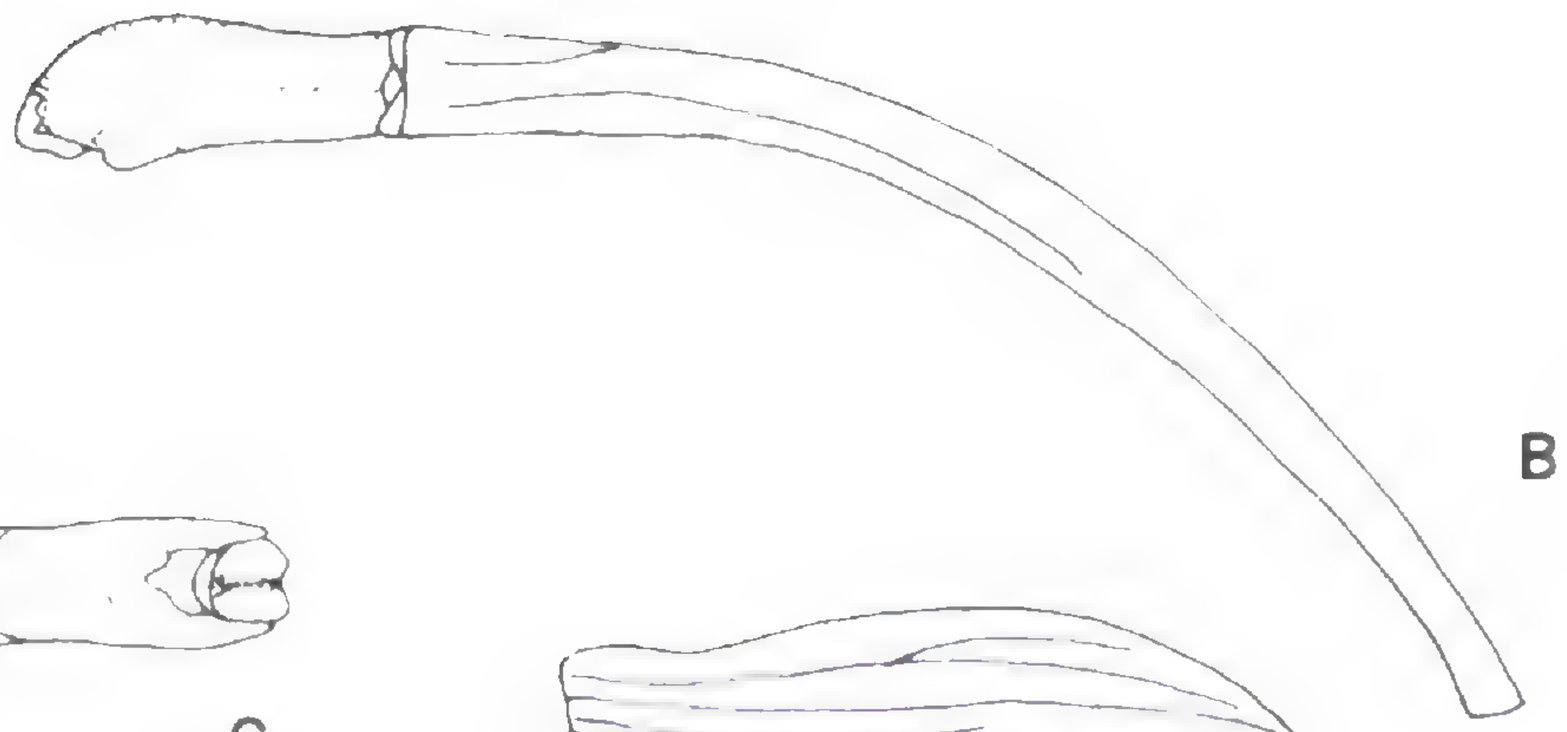

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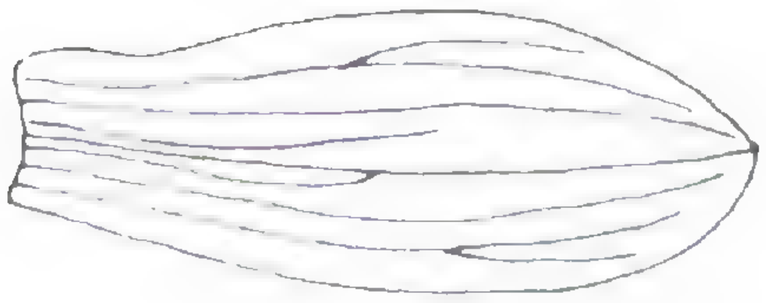

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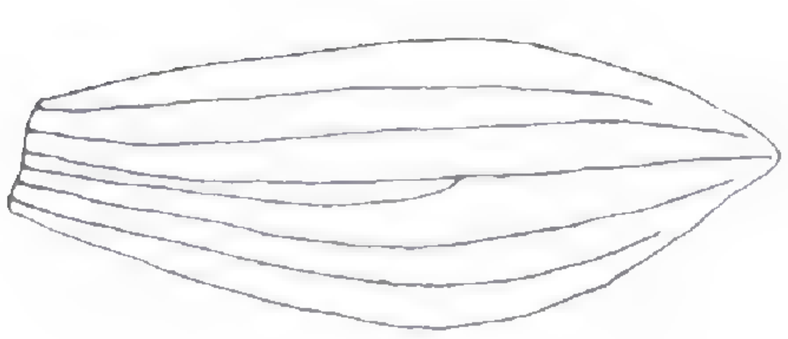

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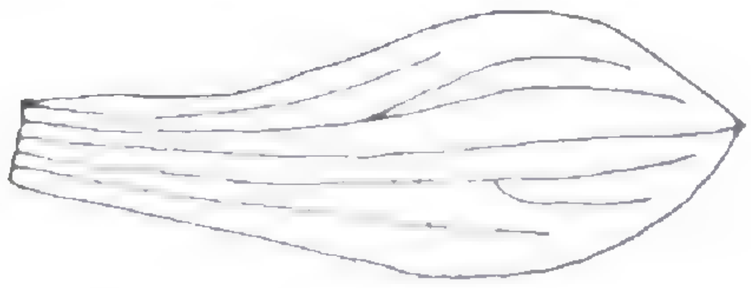

F

5 mm

Figure 7. *Encyclia fucata* (Lindl.) Britton and Millspaugh. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

basally enclosed by fugacious scarious sheaths, to 3-leaved at apex; leaves coriaceous to rigid, linear-lanceolate, acute, to 30 cm long, 2 cm wide; inflorescence terminal, to 75 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 50 flowers; floral bracts minute, ovate, acuminate, to 3 mm long, 2 mm wide; ovary pedicellate, slender, to 2 cm long; sepals greenish-yellow with reddish-brown striping towards apex, oblanceolate to spatulate, acute, to 12 mm long, 3 mm wide; petals greenish-yellow with reddish-brown striping towards apex, oblong to oblanceolate, acute, to 12 mm long, 3 mm wide; labellum free, deeply 3-lobed, to 15 mm long, 10 mm wide, white to yellowish-white with radiating purple lines on lateral lobes, midlobe with a central purple spot, lateral lobes oblong to ligulate, obtuse, converging to embrace and conceal column, midlobe rounded, emarginate, margin undulate, callosity under column is two lateral erect keels joined by a third keel at junction of lobes; column white, stout, short, to 5 mm long, 3 mm wide, auricles absent, anther yellow; capsule pendent, to 13 mm long, 10 mm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** low coppice, Abaco Heights, 28 May 1979, *Sauleda and Correll 2507* (USF); Snake Cay, low coppice, 12 April 1979, *Sauleda and Correll 2311*(FAU); Great Cistern, 14 Dec. 1904, *Brace 1681* (F, NY). **Andros,** Driggs Hill, 10 May 1975, *Sauleda 1052* (F), *1053* (F); high coppice, 6 mi NW of Love Hill settlement, 25 May 1975, *Sauleda 1065* (FAU); freshwater swamp, 2 mi E of Mastic Point, 6 Nov. 1976, *Sauleda 1354* (SEL); island coppice, 9 mi NW of Fresh Creek, 21 Jan. 1977, *Sauleda 1540* (FAU); low coppice, 2 mi N of Love Hill settlement, 5 Feb. 1977, *Sauleda 1838* (FAU); mangrove swamp, around lake 1 mi NW of Love Hill settlement, 20 March 1977, *Sauleda 1878* (FAU); Conch Sound, 22 May 1890, *Northrop and Northrop 584* (AMES, F, NY); Cedar Coppice, 7 May 1978, *Sauleda, Correll, Stevenson and Eckenwalder 2087* (FAU); base of rock hill, 1.5 mi N of Owens Town, 8 May 1978, *Sauleda, Correll, Stevenson and Eckenwalder 2116* (FAU); high coppice, 6 mi NW Love Hill settlement, 17 May 1978, *Sauleda, Correll, Austin and Adams 2121* (MO), *2122* (P), 2123 (W); island coppice, 9 mi NW Fresh Creek, 17 May 1978, *Sauleda, Correll, Austin and Adams 2124* (M), *2125* (LE). *Bimini Group,* **South Bimini,** along runway, 16 Feb. 1979, *Sauleda, Adams, Adams and Correll 2201* (FAU). **Grand Bahama,** John Hill Creek, 16 April–8 May 1905, *Brace 3713* (F, NY).

ADDITIONAL DISTRIBUTION: **Cuba,** *Jack 7991* (NY), Isle of Pines, *Taylor 80* (NY).

REPRODUCTIVE PERIOD: April through September.

ECOLOGY: This species grows epiphytically on *Coccoloba diversifolia* Jacq., *Manilkara bahamensis* (Baker) Lam. & Meese, *Savia bahamensis* Britton, *Conocarpus erectus* L., *Rhizophora mangle* L.

Erythroxylum areolatum L., *Calyptranthes pallens* (Poir.) Griesb., *Ateramnus lucidus* (Sw.) Rothm., *Nectandra coriacea* (Sw.) Griesb., *Annona glabra* L., and *Chrysobalanus icaco* L. The habitats within which this species is found are High Coppice, Low Coastal Coppice, Mangrove Forest, and Freshwater Swamp.

8. **Encyclia gracilis** (Lindl.) Schltr., Die Orchideen, 209. 1915 (Fig, 8).

Basionym: *Epidendrum gracile* Lindl., Bot. Reg. 21:pl.1765. 1835. HOLOTYPE: Bahamas, *Lees s.n.* (K-L, photograph seen).

Encyclia diurna auct. non (Jacq.) Britton & Millspaugh; Britton & Millspaugh, Bahama Fl. 92. 1920.

Epidendrum altissimum auct. non Batem. ex Lindl.; Britton & Millspaugh, Bahama Fl. 92. 1920.

Epidendrum virens auct. non Lindl.; Britton & Millspaugh, Bahama Fl. 92. 1920.

Plant predominantly epilithic, rarely epiphytic, rhizomatous, to 150 cm tall; roots many, thick, canescent; primary stem or rhizome short, stout, creeping, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect, clustered, elongated, ovate to subulate, to 10 cm long, 5 cm thick, basally enclosed by scarious sheaths, to 4-leaved at apex; leaves coriaceous, stiff, erect, linear to linear-lanceolate, acute, to 35 cm long, 4 cm wide, leaf base with pseudobulbous bulges and lacking abscission layer; inflorescence terminal, to 130 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 45 flowers; floral bracts ovate-triangular, acute, concave, to 5 mm long, 5 mm wide; ovary pedicellate, slender, to 2.4 cm long; sepals yellowish-orange with brown striping, elliptic to oblong, acute, to 2.2 cm long, 6 mm wide; petals yellowish-orange with reddish-brown striping toward apex, obovate to spatulate, acute to obtuse, to 2.0 cm long, 5 mm wide; labellum free, deeply 3-lobed, to 2.2 cm long, 2.4 cm wide, white with radiating purple lines on lobes, lateral lobes oblong, obtuse, erect, embracing column, midlobe rounded, emarginate, margin undulate, callosity under column is two lateral erect keels joining at junction of lobes; column white to yellowish-white, streaked with purple, elongate, to 10 mm long, 5 mm wide, with membranaceous incurved rounded auricles, anther yellow; capsule pendent, to 2.5 cm long, 1.5 cm thick.

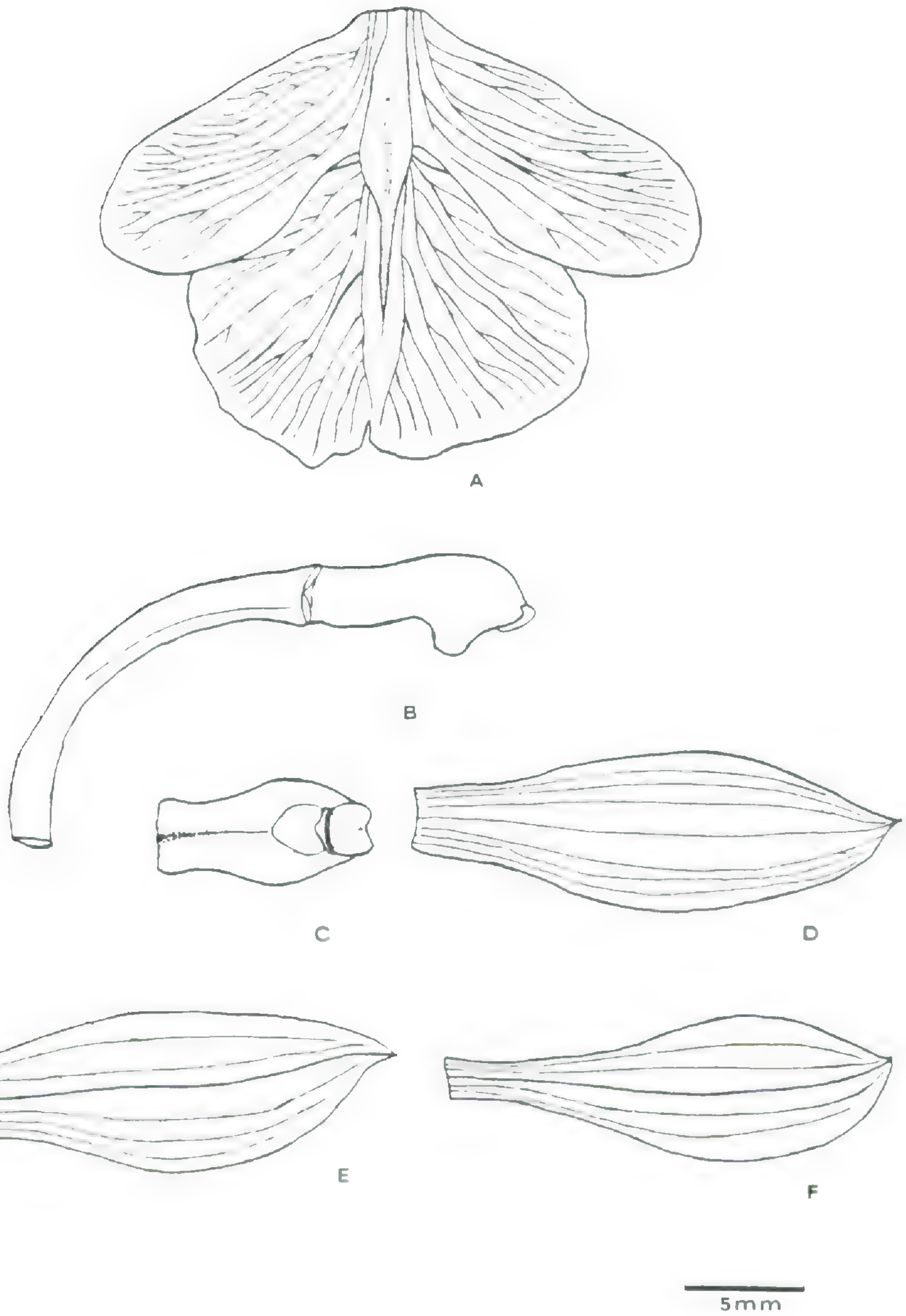

Figure 8. *Encyclia gracilis* (Lindl.) Schltr. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** Abaco Heights, low coppice, 11 April 1979, *Sauleda and Correll 2258* (FAU); Snake Cay, low coppice, 12 April 1979, *Sauleda and Correll 2312* (FAU); coastal coppice near Treasure Cay, 6 July 1974, *Correll, Popenoe and Patterson 42668-A* (FTG); Guana Bight, 1 July 1948, *McSwinney s.n.* (AMES). **Andros,** rock scrub, 9.5 mi S of Fresh Creek, 15 Oct. 1976, *Sauleda 1138* (FAU); rock scrub, 8 mi S of Fresh Creek, 15 Oct. 1976, *Sauleda 1139* (SEL), *1140* (FTG), *1141* (P), *1146* (AMES), *1147* (NY), *1149* (FAU), *1151* (S), *1153* (W), *1154* (K), *1155* (F), *1156* (F), *1157* (US), *1158* (MO); island coppice, 9 mi NW of Fresh Creek, 21 Jan. 1977, *Sauleda 1531* (FAU); low coppice, 2 mi N of Love Hill settlement, 16 April 1977, *Sauleda 1866* (FAU); rock scrub, 9 mi S of Fresh Creek, 16 April 1977, *Sauleda 1867* (FAU); Cedar Coppice, 7 May 1978, *Sauleda, Correll, Stevenson and Eckenwalder 2088* (FAU); mangrove swamp, 6 Nov. 1976, *Adams 2002* (FAU); Deep Creek, 17 Aug.–10 Sept. 1906, *Brace 5149* (AMES, F, NY, US); Bigwood Cay, 12 July 1975, *Hill 3406* (FTG); Mangrove Cay, near Moxey Town, 8 Aug. 1979, *Sauleda 2879* (FAU). **Eleuthera,** Silver Palm coppice area, 11 Aug. 1977, *Correll and Correll 48926* (FTG); along roadside at Deep Creek, 4 June 1979, *Sauleda 2709* (FAU). **Cat Island,** dunes, 2.5 mi E of airport, 21 Jan. 1979, *Sauleda and Correll 2194* (FAU). **Crooked Island,** Turtle Sound Landing, 5 June 1977, *Correll and Proctor 48733* (FTG). **Exuma Chain,** Norman's Cay, near airport, 18 Jan. 1979, *Sauleda and Correll 2180* (FAU); Ship Channel Cay, 17 Feb. 1905, *Britton and Millspaugh 2749* (NY). **Grand Bahama,** Eight Mile Rocks, 16 April–8 May 1905, *Brace 3735* (NY, US); Freeport, west end of airstrip, 25 May 1975, *Correll, Popenoe and Fluck 45444* (FTG). **Great Inagua,** Blakes Wells, 24 June 1978, *Sauleda, Adams, Adams and Correll 2143* (FAU). **Long Island,** Moss Hill, 7–17 Dec. 1905, *Brace 4237* (NY). **New Providence,** White Lands race course, 26 Aug. 1904, *Britton and Brace 280* (AMES, F, MO, NY, US); south of Fox Hills, 5 Sept. 1904, *Britton and Brace 536* (F, NY), 5 Sept. 1904, *Britton and Brace 544* (NY).

DISTRIBUTION IN THE TURKS AND CAICOS ISLANDS: **Middle Caicos,** on road between Nango and Free Town, *Sauleda, Adams and Correll 2032* (FAU), *2033* (FAU).

REPRODUCTIVE PERIOD: June through November.

ECOLOGY: This species is found growing mainly epilithically on Pleistocene limestone and occasionally epiphytically at the base of *Aterammus lucidus* (Sw.) Rothm., *Buxus bahamensis* Baker, and *Strumpfia maritima* Jacq. The habitats in which it is found are Beach and Dune, Coastal Rock Scrub, Low Coastal Coppice, Inland Scrub, and in open sunny disturbed areas in High Coppice. Endemic.

9. **Encyclia hodgeana** (Hawkes) Beckner, Phytologia **20**: 217. 1970 (Fig. 9).

Basionym: *Epidendrum altissimum* Batem. ex Lindl., Bot. Reg. **24**: Misc. 38, 1838, non Jacq. 1760.

Epidendrum hodgeanum Hawkes, Orquidea **18**: 176. 1956.

Encyclia altissima (Batem. ex Lindl.) Schltr., Die Orchideen 207. 1915.
HOLOTYPE: Bahamas, *Skinner s.n.* (K–L, photograph seen).
Encyclia diurna auct. non (Jacq.) Britton & Millspaugh; Britton & Millspaugh, Bahama Fl. 92. 1920.
Epidendrum gracile auct. non Lindl.; Britton & Millspaugh, Bahama Fl. 92. 1920.
Epidendrum virens auct. non Lindl.; Britton & Millspaugh, Bahama Fl. 92. 1920.

Plant epiphytic or epilithic, rhizomatous, to 245 cm tall; roots many, slender to thick, velamentous or canescent; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect, clustered, e gated, linear-lanceolate to lanceolate, attenuate, to 60 cm long, 8 cm thick, enclosed by scarious imbricating sheaths, to 4-leaved at apex; leaves coriaceous to rigid, linear to linear-lanceolate, acute, to 60 cm long, 3.5 cm wide; inflorescence terminal, to 185 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 40 flowers; floral bracts ovate-triangular, acute, to 3 mm long, 3 mm wide; ovary pedicellate, slender, to 2.5 cm long; sepals greenish-tan with dark brown striping, elliptic, acute, to 2.2 cm long, 7 mm wide; petals greenish-tan with reddish-brown striping towards apex, oblanceolate, acute, to 2.2 cm long, 4 mm wide; labellum free, deeply 3-lobed, to 2.8 cm long, 2.2 cm wide, lateral lobes yellow with radiating purple lines, oblong, obtuse, erect, embracing column, midlobe white with yellow undulating margin, marked with purple radiating lines, callosity under column is two lateral erect keels joining at midlobe, two undulate lamellae parallel keel on midlobe; column white, streaked with purple, elongate, to 1.8 cm long, 5 mm wide, with membranaceous incurved rounded auricles, anther yellow; capsule pendent, to 2.5 cm long, 2.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** edge of high coppice, 3.1 mi N Treasure Cay airport, 3 Aug. 1979, *Sauleda, Adams and Adams 2839* (FAU); Snake Cay, low coppice, 12 April 1979, *Sauleda and Correll 2310* (FAU); Cherokee Sound, 29 Dec. 1904, *Brace 1936* (F, NY); coppice, Cherokee settlement, 31 Dec. 1904 *Brace 1992* (NY). **Acklin's Island,** Spring Point, 21 Dec. – 6 Jan. 1906, *Brace 4315* (AMES, F). **Andros,** rock scrub, 8 mi S of Fresh Creek, 21 Jan. 1977, *Sauleda 1516* (SEL), *1519* (F), *1521* (S); island coppice, 9 mi NW of Fresh Creek, 21 Jan. 1977, *Sauleda 1523* (FAU); rock scrub, 9 mi S of Fresh Creek, 21 Jan. 1977, *Sauleda 1538* (FAU); low coppice, 2 mi N of Love Hill settlement, 5 Feb. 1977,

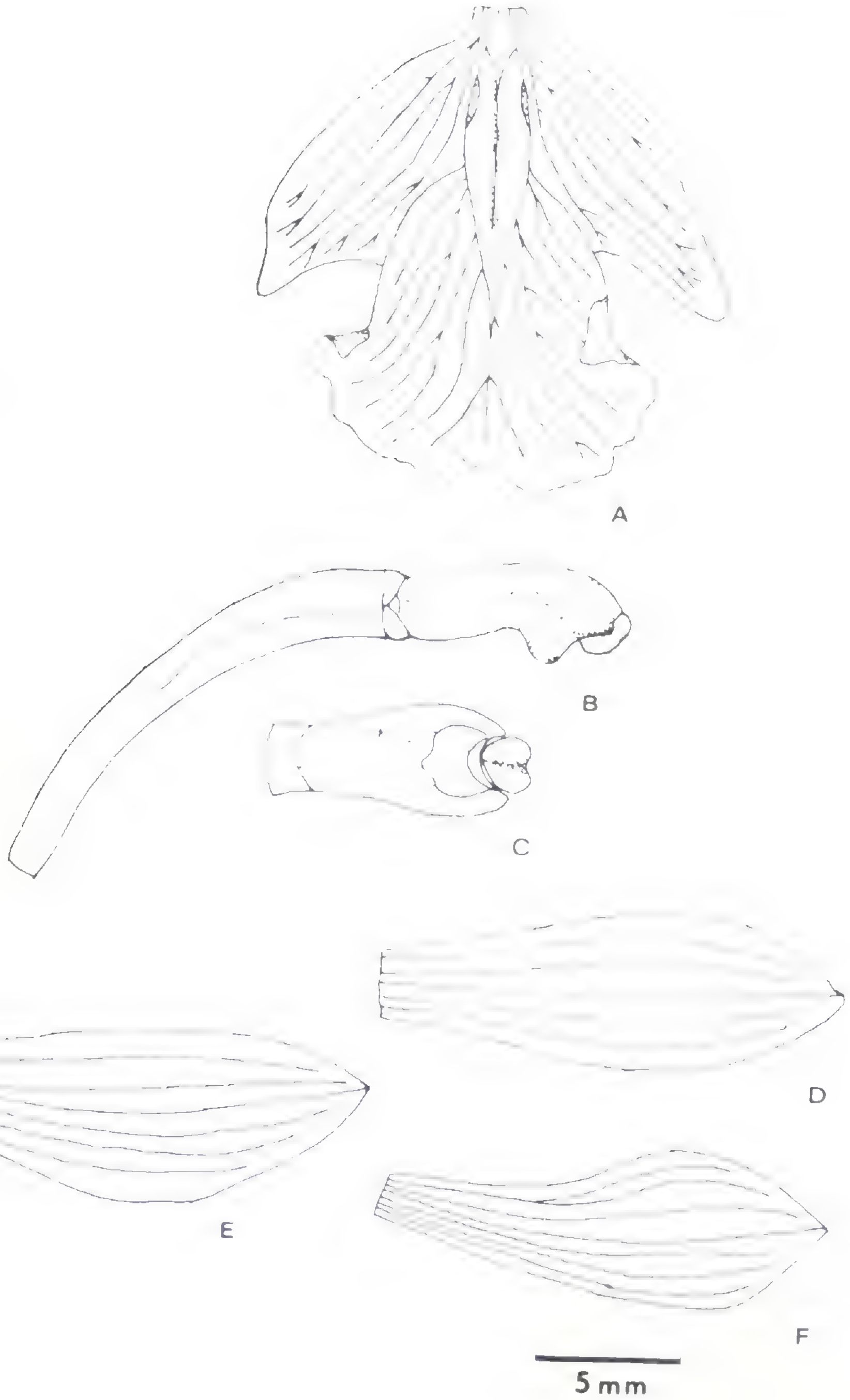

Figure 9. *Encyclia hodgeana* (Hawkes) Beckner. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

Sauleda 1833 (FAU); 3 mi N of Cargil Creek, 7 March 1966, *Dawson 26749* (US); Deep Creek, 20-22 Jan. 1910, *Small and Carter 8542* (AMES, F, NY); Mangrove Cove, between airport and Moxey Town, 22 July 1978, *Sauleda and Correll 2144* (FAU). **Cat Island,** low coppice, 2 mi. S of Stevenson, 19 Jan. 1977, *Sauleda, Correll and Correll 2183* (FAU); the Bight and vicinity, 22 23 Nov. 1907, *Wilson 7181* (F, MO, NY). **Crooked Island,** Landrail Point, 9–23 Jan. 1906, *Brace 4527* (AMES, F, NY). **Eleuthera,** along roadside at Deep Creek, 4 June 1979, *Sauleda 2708* (FAU); low coppice, 3 mi N of Gregory Town, 2 June 1979, *Sauleda 2652* (FAU); White Lands, 18 Feb. 1907, *Britton and Millspaugh 5421* (F, NY). **Exuma Chain,** Ship Channel Cay, 17 Feb. 1905, *Britton and Millspaugh 2759* (F, NY); cay N of Wide Opening, 18 Feb. 1905, *Britton and Millspaugh 2770* (F, NY, US); Great Exuma, W of Goat Key, 17 Jan. 1979, *Sauleda, Correll and Correll 2173* (FAU); on ground, low coppice, near Rolletown, 27 28 Feb. 1905, *Britton and Millspaugh 3073* (F, NY); Orchid Heights, Hummingbird Cay, 12 Jan. 1970, *Edge and Swain 3240* (MO); Culmer's Cay, 14 Jan. 1970, *Nickerson and Case 3251* (MO); Norman's Cay, near runway, 18 Jan. 1979, *Sauleda and Correll 2177* (FAU); Staniel Cay, near airport, 18 Jan. 1979, *Sauleda and Correll 2181* (FAU). **Inagua Group,** Great Inagua, along runway, 23 June 1978, *Sauleda, Adams, Adams and Correll 2136* (FAU); along airport road, 31 Dec. 1961, *Dunbar 28* (AMES); Little Inagua, SW sector, 12–16 Aug. 1975, *Correll 46009* (FTG). **Long Island,** 2 mi S of Clarence Town, 20 Jan. 1979, *Sauleda and Correll 2189* (FAU); road to south side, 7–17 Dec. 1905, *Brace 4046* (AMES, F, US). **Mayaguana,** Abraham Bay, 10 12 Dec. 1907, *Wilson 7478* (F, NY); Southeast Point, 6 8 Dec. 1907, *Wilson 7589* (F, NY). **New Providence,** low coppice S of Fox Hills, 5 Sept. 1904, *Britton and Brace 548* (NY); coppice, Molf Road, 26 Jan. 1905, *Britton and Millspaugh 2107* (F, NY); Soldier's Road, 25 Jan. 1905, *Millspaugh 2485* (F, NY); 1 mi S of Fox Hills, 18 Jan. 1905, *Wight 2* (AMES); 3 mi SE of Nassau, 19 March 1905, *Wight 344* (AMES). **Rum Cay,** near Port Nelson, 4 Dec. 1905, *Brace 3973* (AMES, F, NY, US). **San Salvador**, Graham's Harbor, 26 Nov. 1907, *Wilson 7251* (US, NY).

DISTRIBUTION IN THE TURKS AND CAICOS ISLANDS: **Middle Caicos,** along road between Free Town and Nango Town, 11 Feb. 1978, *Sauleda, Adams and Correll 2039* (K), *2040* (BR), *2041* (W), *2042* (MO), *2043* (M). **North Caicos,** road to Whitby, 13 Feb. 1978, *Sauleda, Adams, Adams, and Correll 2048* (FAU).

ADDITIONAL DISTRIBUTION: **Haiti,** *Leonard and Leonard 12773* (NY).

REPRODUCTIVE PERIOD: November through March.

ECOLOGY: This species grows epilithically on Pleistocene limestone and epiphytically on *Byrsonima cuneata* (Turez) P. Wilson, *Buxus bahamensis* Baker, *Psidium longipes* (Berg) McVaugh, *Ateramnus lucidus* (Sw.) Rothm., *Juniperus bermudiana* L., *Thovinia discolor* Griesb., *Gochnatia ilicifolia* Less, *Tabebuia bahamensis* (Northrop) Britton, *Coccoloba diversifolia* Jacq., *Savia bahamensis* Britton, and *Coccothrinax argentata* (Jacq.) L.H. Bailey. The habitats in which it is found are Coastal Rock Scrub, Low Coastal Coppice, Inland Scrub, and High Coppice.

10. **Encyclia inaguensis** Nash ex Britton and Millspaugh, Bahama Fl. 92. 1920 (Fig. 10).

TYPE: On trees and shrubs, between Northwest and Southwest Point, Little Inagua, 21 October 1904, *Nash and Taylor 1251* (HOLOTYPE: NY; ISOTYPES: AMES, F).

Plant epiphytic or epilithic, rhizomatous, to 175 cm tall; roots many, slender to thick, velamentous or canescent; primary stem or rhizome short, stout, creeping, usually ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect, clustered, elongated, attenuate, linear-lanceolate, to 31 cm long, 3.5 cm thick, enclosed by scarious imbricating sheaths, to 2-leaved at apex; leaves coriaceous to rigid, linear, acute, to 55 cm long, 1.8 cm wide; inflorescence terminal, to 144 cm tall, peduncle slender, erect, distantly several-sheathed, paniculate above, lateral branches ascending, to 45 flowers; floral bract ovate-triangular, acute, to 8 mm long, 8 mm wide; ovary pedicellate, slender, to 3 cm long; sepals green to greenish-tan with brown to reddish-brown striping, elliptic to oblanceolate, acute, to 1.7 cm long, 7 mm wide; petals green to greenish-tan with brown to reddish-brown striping, oblanceolate, acute, to 2 cm long, 5 mm wide; labellum free, deeply 3-lobed, to 1.9 cm long, 2.0 cm wide, lateral lobes yellow with radiating purple lines, oblong, subacute, erect, embracing column, midlobe yellow to yellowish-green, center of disc marked with purple radiating lines, margin undulate, callosity under column composed of two dents decurrent in erect keels joining at midlobe, purple; column white, streaked with purple, elongate, to 1.8 cm long, 5 mm wide with membraneous, incurved, rounded auricles, anther yellow; capsule pendent, to 3.0 cm long, 2.2 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Little Inagua,** along trail from western shore to Royal Palm sinkholes, 16 July 1976, *Correll 47348* (FTG); between Northwest and Southwest Point, 21 October 1904, *Nash and Taylor 1251* (AMES, F, NY), *1255* (NY).

DISTRIBUTION IN THE TURKS AND CAICOS ISLANDS: **Providenciales,** between Five Cays and Blue Hills, 11 July 1954, *Proctor 9149* (AMES). **Middle Caicos,** along road between Free Town and Nango town, 11 Feb. 1978, *Sauleda, Adams and Correll 2035* (NY), *2036* (FAU), *2037* (US), *2038* (K). **North Caicos,** along road at Bellfield Landing, 12 Feb. 1978, *Sauleda, Adams, Adams and Correll 2050* (FAU); James Hill, 12 Feb. 1978, *Sauleda, Adams, Adams and Correll 2053* (AMES, F, FAU).

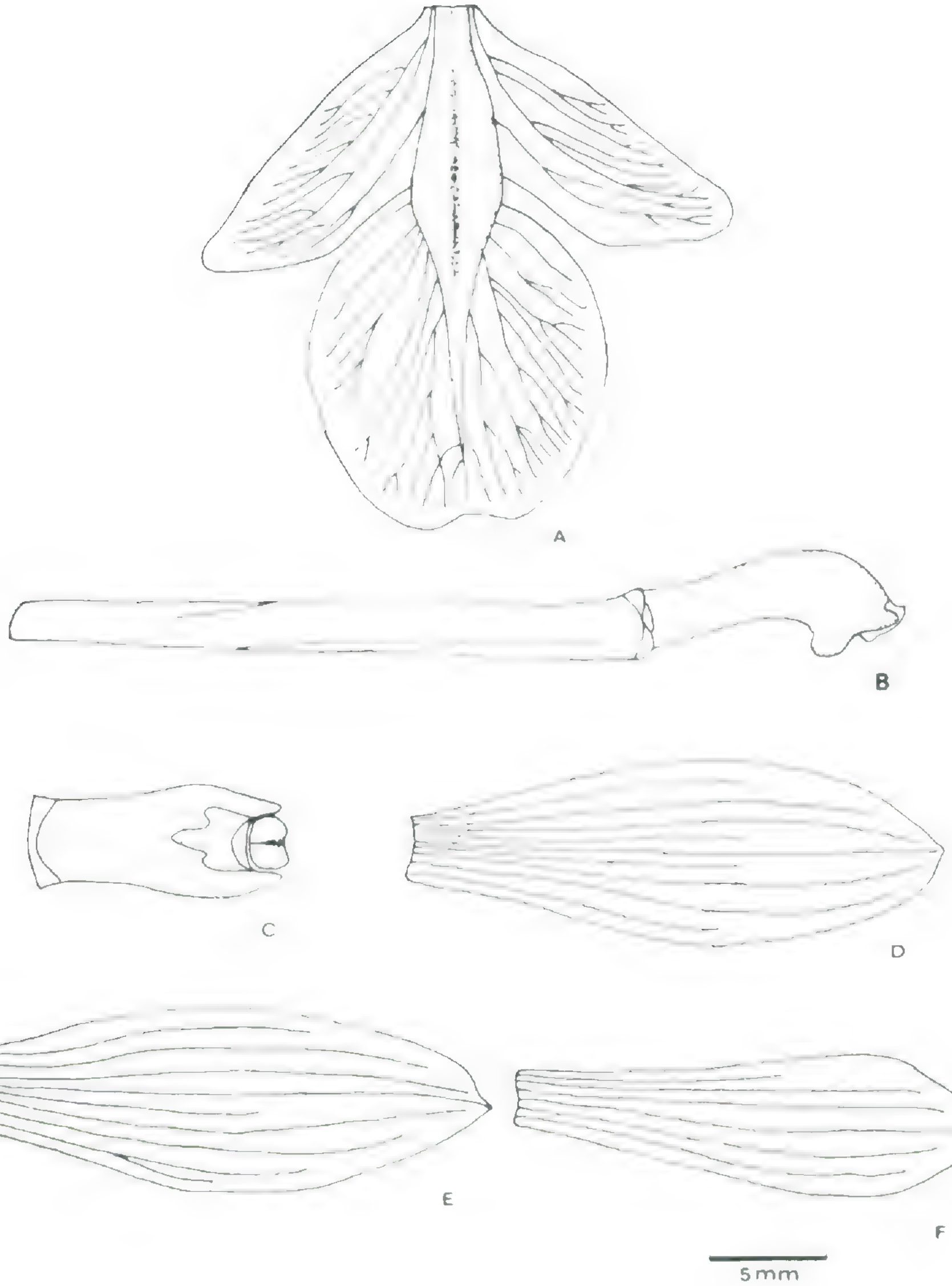

Figure 10. *Encyclia inaguensis* Nash ex Britton and Millspaugh. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

REPRODUCTIVE PERIOD: July through October.

ECOLOGY: On Little Inagua and the Caicos Group this species is found growing epilithically and occasionally epiphytically on *Leucaena leucocephala* (Lam.) DeWit and *Aterammus lucidus* (Sw.) Rothm. The habitats in which it is found are Coastal Rock Scrub and Low Coastal Coppice. Endemic.

ADDITIONAL COMMENTS: *Encyclia inaguensis* is similar to and may be confused with immature or nonreproductive plants of *Encyclia hodgeana* (Hawkes) Beckner. *Encyclia inaguensis* usually has a single leaf which is distinctly narrower. Florally, these two species differ significantly in the shape of the midlobe of the labellum. In *E. hodgeana* the disc is flattened while in *E. inaguensis* the lateral edges are reflexed.

11. **Encyclia plicata** (Lindl.) Britton & Millspaugh, Bahama Fl. 92. 1920 (Fig. 11).

Basionym: *Epidendrum plicatum* Lindl., Bot. Reg. **33**:pl. 35. 1847. Holotype: Cuba, *Loddiges s.n.* (K–L, photograph seen).

Plant epiphytic or epilithic, rhizomatous, to 75 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, ovate, attenuate toward apex, to 6 cm long, 4 cm wide, enclosed by scarious sheaths, to 3-leaved at apex; leaves coriaceous to rigid, erect, linear to linear-lanceolate, acute, to 35 cm long, 2.4 cm wide; inflorescence terminal, to 69 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 30 flowers; floral bracts ovate-triangular, acute to 3 mm long, 4 mm wide; ovary pedicellate, slender, to 2.4 cm long; sepals green, yellow, or brownish-orange, usually with reddish-brown suffusion, elliptic to linear-lanceolate, to 2.5 cm long, 1 cm wide; petals green, yellow or brownish-orange, usually with reddish-brown striping toward apex, oblanceolate to spatulate, acute to acuminate, to 2.2 cm long, 8 mm wide; labellum free, deeply 3-lobed, to 3 cm long, 3 cm wide, white to purple with reddish-purple radiating lines on lobes, lateral lobes, narrowly triangular, obtuse, erect, converging to embrace and conceal column, midlobe cordate to suborbicular, emarginate,

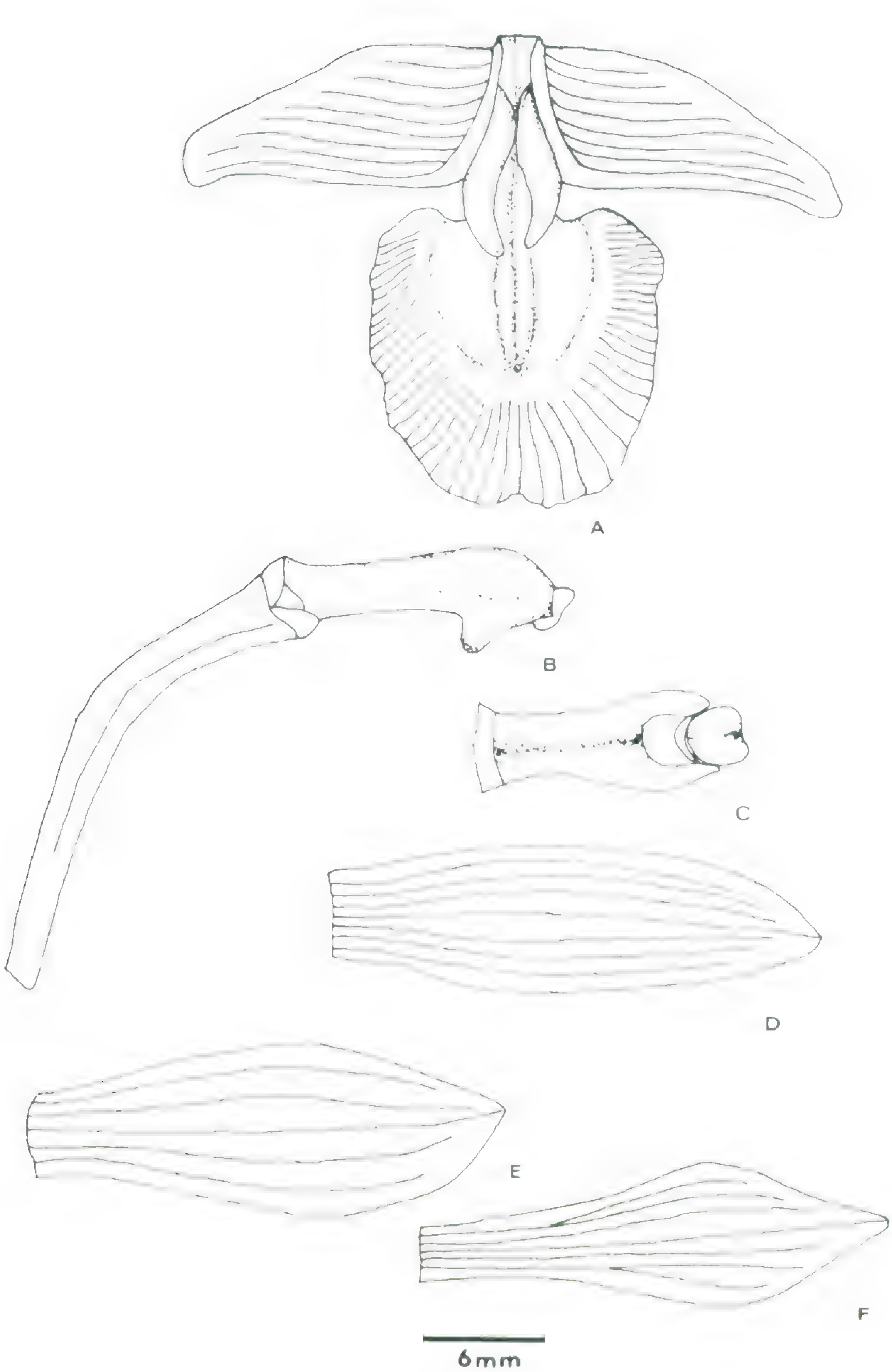

Figure 11. *Encyclia plicata* (Lindl.) Britton and Millspaugh. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

usually reflexed or strongly pleated, margin undulate, with two fleshy pads spreading from base of disc, callosity under column is two thick fleshy lateral erect keels terminating at base of disc in two tubercles; column white or purple, elongate, to 1.4 cm long, 6 mm wide, with membranaceous, incurved pointed auricles, anther white or purple; capsule pendent, to 4 cm long, 2.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** W of Treasure Cay, 6 July 1974, *Correll, Popenoe and Patterson 42688* (FTG). **Andros,** low coppice, N of Fresh Creek, 10 May 1975, *Sauleda 1033* (AMES), *1056* (SEL); mangrove around lake 1 mi NW of Love Hill settlement, 15 Oct. 1976, *Sauleda 1167* (K), *1168* (F); island coppice, 9 mi NW of Fresh Creek, 21 Jan. 1977, *Sauleda 1532* (FAU); high coppice, 6 mi NW of Fresh Creek, 16 April 1977, *Sauleda 1884* (FAU); Mangrove Cay, 18 Aug. –10 Sept. 1906, *Brace 4919* (AMES, NY); Bearing Point, 18 Aug. – 10 Sept. 1906, *Brace 5315* (NY); Fresh Creek, 11 June 1890, *Northrop and Northrop 609* (AMES, F, NY); Deep Creek, 20 –22 Jan. 1910, *Small and Carter 8541* (F, NY). **New Providence,** on *Annona,* swamp, Clifton, 13 Sept. 1904, *Britton and Brace 752* (NY).

ADDITIONAL DISTRIBUTION: **Cuba,** *Leon 14964* (NY).

REPRODUCTIVE PERIOD: May through September.

ECOLOGY: This species is found growing occasionally epilithically on Pleistocene limestone and mainly epiphytically on *Erythroxylum areolatum* L., *Ateramnus lucidus* (Sw.) Rothm., *Tabebuia bahamensis* (Northrop) Britton, *Petitia domingensis* Jacq., *Picrammia pentandra* Sw., *Bourreria ovata* Miers, *Randia aculeata* L., *Zanthoxylum coriaceum* A. Rich., *Coccoloba northropiae* Britton, *Schaefferia frutescens* Jacq., *Casearia bahamensis* Urban, *Savia bahamensis* Britton, *Tetrazygia bicolor* (Mills.) Cogn., *Manilkara bahamensis* (Baker) Lam. & Meese, *Crossopetalum rhacoma* (Sw.) Hitchc., *Psidium longipes (Berg) McVaugh, Juniperus bermudiana* L., *Terebraria resinosa* (Vahl.) Sprague, *Coccoloba diversifolia* Jacq., *Rhizophora mangle* L., *Coccoloba tenuifolia* L., *Lysiloma latisiliqua* (L.) Benth., *Acacia choriophylla* Benth., *Calyptranthes zuzygium* (L.) Sw., and *Hypelate trifoliata* Sw. The habitats in which it is found are Low Coastal Coppice, Mangrove Forest, and High Coppice.

12. **Encyclia rufa** (Lindl.) Britton & Millspaugh, Bahama Fl. 91. 1920 (Fig. 12).

Basionym: *Epidendrum rufum* Lindl., Bot. Reg. **31**: Misc. 33.

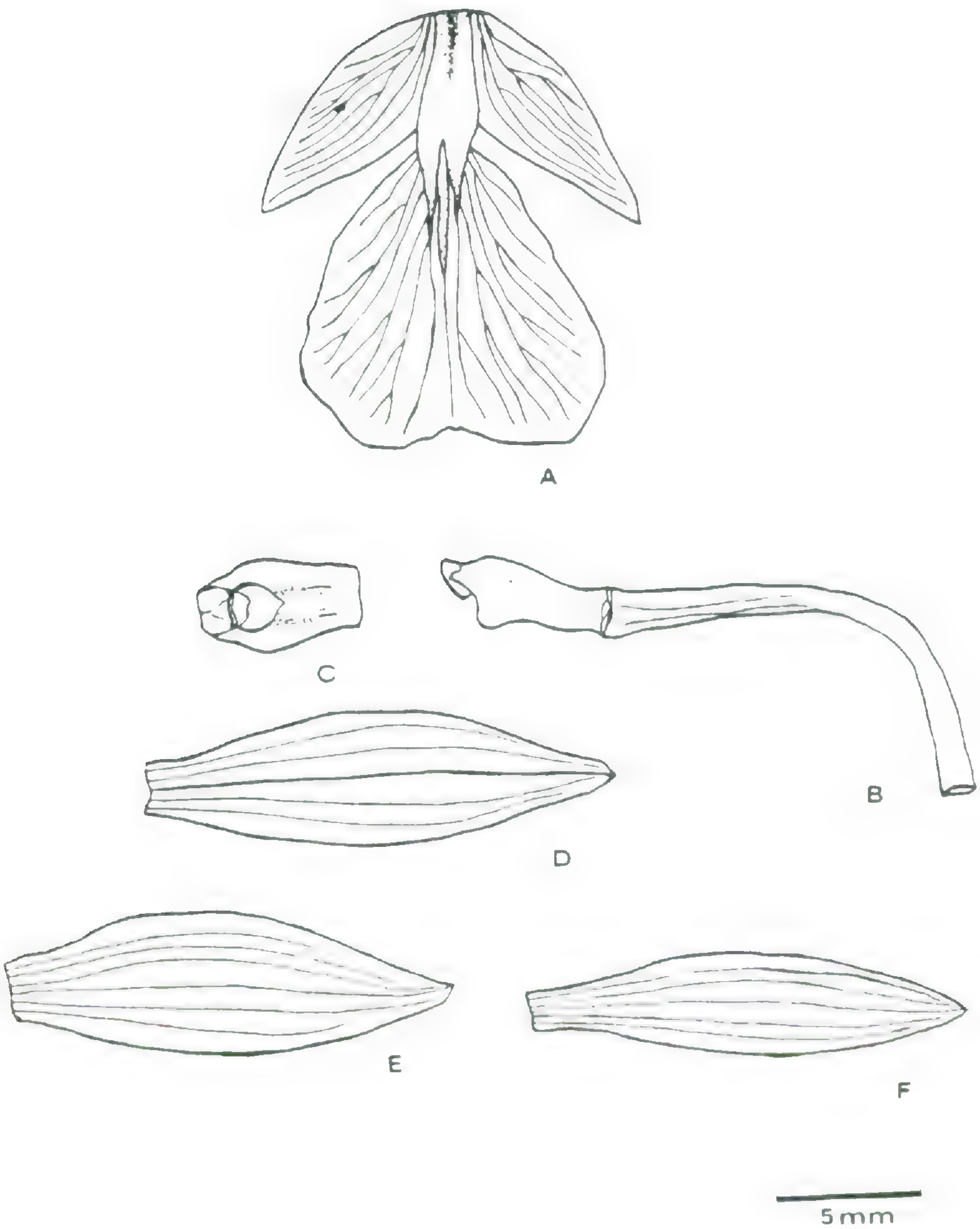

Figure 12. *Encyclia rufa* (Lindl.) Britton and Millspaugh. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

1845. Holotype: Brazil, *Turner s.n.* (K–L, photograph seen).

Epidendrum bahamense Griesb., Fl. Br. W.I. 614. 1864.

Encyclia bahamensis (Griesb.) Britton & Millspaugh, Bahama Fl. 91. 1920. Holotype: Bahamas, *Swains s.n.* (K, photograph seen).

Epidendrum primulinum Batem. ex Lindl., in Paxton's Fl. Gard. **I**: 151. 1853. Holotype: Mexico, *no collector* (K–L, photograph seen).

Epidendrum odoratissimum auct. non Lindl.; Northrop, Mem. Tor. Bot. Cl. **12**: 29. 1902.

Plant epiphytic or epilithic, rhizomatous, to 90 cm tall; roots numerous, slender, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, ovate, attenuate toward apex, to 12 cm long, 7 cm wide, enclosed by scarious sheaths, to 3-leaved at apex; leaves coriaceous to rigid, linear to linear-lanceolate, acute, to 36 cm long, 2.5 cm wide; inflorescence terminal, to 78 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, lateral branches stiff and erect, to 50 flowers; floral bracts ovate-triangular, acute, concave, to 2 mm long, 3 mm wide; ovary pedicellate, slender, to 2 cm long, sepals green to yellow, occasionally with reddish-brown suffusion, glossy, obovate to oblanceolate, acute, to 1.8 cm long, 6 mm wide; petals green to yellow, occasionally with reddish-brown striping toward apex, glossy, elliptic to oblanceolate, acute, to 1.8 cm long, 5 mm wide; labellum free, 3-lobed, to 1.8 cm long, 1.6 cm wide, green or yellow, occasionally yellow or white with radiating purple lines, lateral lobes oblong, obtuse, erect, embracing column, midlobe round to obovate, emarginate or apiculate, recurved. lateral margins revolute, callosity under column is two lateral erect keels occasionally joined by a third keel at junction of lobes; column white or green, occasionally streaked with purple, short, to 6 mm long, 4 mm wide, with membranaceous square auricles, anther white; capsule pendent, to 2.5 cm long, 2.0 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** 3.1 mi N of Treasure Cay airport, 3 Aug. 1979, *Sauleda, Adams and Adams 2841* (FAU); Eight Mile Bay, 26 Dec. 1904, *Brace 1875* (F, NY); Cherokee Sound, 28 Dec. 1904, *Brace 1906* (F, NY). **Little Abaco,** near Fox Cay settlement, 3 Aug. 1979, *Sauleda, Adams and Adams 2865* (FAU). **Andros,** low coppice, on west bank of Stafford Creek, 15 Oct. 1976, *Sauleda 1137* (FAU); island coppice, 9 mi NW of Fresh Creek, 16 April 1977,

Sauleda 1853 (S), *1854* (F), *1855* (K), *1856* (LE), *1857* (W), *1858* (MO), *1859* (P); palm forest, 12 mi W of Fresh Creek, 16 April 1979, *Sauleda 1885* (FAU); Calabash Bay, 6 June 1890, *Northrop and Northrop 606* (F, NY); near Staniard Creek, 1–2 Feb. 1910, *Small and Carter 8892* (NY, US). **Bimini Group,** Easter Key, May, 1948, *Howard and Howard 10276* (NY); South Bimini, May 1948, *Howard and Howard 10277* (NY); North Bimini, coppice past town, 21 April 1979, *Sauleda 2341* (USF). **Cat Island,** low coppice, 2 mi S of Stevenson, 19 Jan. 1979, *Sauleda, Correll and Correll 2184* (FAU); the Bight and vicinity, 22 23 Nov. 1907, *Wilson 7170* (F, NY). **Crooked Island,** Landrail Point, 9–23 Jan. 1906, *Brace 4642* (F, NY, US). **Eleuthera,** Cape Eleuthera, low coppice, 4 June 1979, *Sauleda 2719* (FAU); The Current, palm forest, 2 June 1979, *Sauleda 2679* (FAU); near landing, road to the Bluff, 18 Feb. –4 March 1907, *Britton 6419* (F, NY); Sunshine coppice, 18 Feb. 1906, *Britton and Millspaugh 5428* (F); The Current, 5 July 1903, *Coker 351* (NY).

Exuma Chain, Great Exuma, W of Moss Town, 22 June 1978, *Sauleda, Adams, Adams and Correll 2132* (B); Ship Channel Cay, 17 Feb. 1905, *Britton and Millspaugh 2756* (F, NY); Jewfish Cay, 10 June 1970, *Gillis 9365* (MO); Orchid Heights, Hummingbird Cay, 2 April 1968, *Kessler, Nickerson and Sammons 2752* (MO). **Grand Bahama,** road to Deadman's Reef, 16 April –8 May 1906, *Brace 3620* (F, NY). **Inagua Group,** Great Inagua, near Union Creek, 24 June 1978, *Sauleda, Adams, Adams, and Correll 2139* (L); 8 May 1935, *Fairchild and Dorsett 99054* (AMES); white land, 14 Feb. 1904, *Nash and Taylor 1049* (NY); Little Inagua, Oct. 1904, *Nash and Taylor 1252* (NY); Alfred Sound, 31 May 1974, *Proctor and Gillis 33866* (MO). **Long Island,** low coppice, 2 mi S of Clarence Town, 20 Jan. 1979, *Sauleda and Correll 2188* (FAU); dry coppice W of Clarence Town, 9 May 1970, *Hill 532* (US). **New Providence,** Southside Beach, 31 Aug. 1904, *Britton and Brace 385* (F, NY, US); coppice S of Fox Hills, 5 Sept. 1904, *Britton and Brace 541, 546* (NY). **San Salvador,** Sandy Hook, south side of island, 15 June 1978, *Smith, Horgan, and Rumansky s.n.* (FTG). **Berry Islands,** Chub Cay, 1 mi E of runway, 21 April 1978, *Sauleda, Correll and Eckenwalder 2061* (L), *2062* (M), *2063* (B), *2064* (BM), *2065* (BR); Great Harbor Cay, off Pirate's Way, 17 Oct. 1974, *Correll and Correll 43722* (FTG); low coppice, Stede Bonnet road, 12 May 1979, *Sauleda and Correll 2469* (USF).

DISTRIBUTION IN THE TURKS AND CAICOS ISLANDS: **Middle Caicos,** road between Free Town and Nango Town, 11 Feb. 1978, *Sauleda, Adams and Correll 2034* (FAU). **North Caicos,** Bellfield Landing, 12 Feb. 1978, *Sauleda, Adams, Adams and Correll 2049* (FAU); James Hill, *Sauleda, Adams, Adams and Correll 2051* (FAU); Whitby's Landing, 28 Feb.—2 March 1911, *Millspaugh and Millspaugh 9164* (F, NY). **Providenciales,** open coppice on Hills, Long Bay, 18 Dec. 1975, *Correll 46402* (FTG).

REPRODUCTIVE PERIOD: May through July.

ECOLOGY: This species is found growing epilithically on Pleistocene limestone and epiphytically on *Bumelia salicifolia* (L.) Sw., *Coccoloba diversifolia* Jacq., *Acacia choriophylla* Benth., *Pithecellobium guadalupense* (Pers.) Chapm., and *Coccothrinax argentata* (Jacq.) L.H. Bailey. The habitats in which it is found are Beach and Dune, High Coppice, Low Coastal Coppice, Coastal Rock Scrub, and Inland Scrub.

ADDITIONAL COMMENTS: We question the veracity of the Brazilian locality cited for the holotype of this species, since no other specimens of *Epidendrum (= Encyclia) rufa* have ever been collected in Brazil. Additionally, we question the accuracy of the Mexican locality cited for the holotype of *Epidendrum primulinum*, a synonym of *E. rufa*. No other specimens of *E. rufa* have ever been collected in Mexico. A single specimen of *E. rufa (Small, Mosier and Matthaus, 12938)* collected 24 May 1926 in a Hammock N of Eau Gallie, Brevard County, Florida is extant in NY. We believe that this specimen was probably introduced by travelers from the Bahamas since no other reports of the presence of *E. rufa* in Florida are extant. We are convinced that the distribution of *E. rufa* is restricted to the Bahama archipelago and Cuba.

13. **Encyclia selligera** (Batem. ex Lindl.) Schltr., Die Orchideen 211. 1914 (Fig. 13).

Basionym: *Epidendrum selligerum* Batem. ex Lindl., Bot. Reg. **24**: Misc. 40. 1838. HOLOTYPE: Guatemala, *Skinner s.n.* (K–L, photograph seen).

Plant epiphytic, rhizomatous, to 65 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, ovoid to ovate, to 6 cm long, 4 cm wide, enclosed by scarious sheaths, to 3-leaved at apex; leaves coriaceous to rigid, erect, linear-ligulate, obtuse to acute, to 28 cm long, 2.4 cm wide; inflorescence terminal, to 59 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 30 flowers; floral bracts ovate-triangular, acute, to 4 mm long, 5 mm wide; ovary pedicellate, slender, to 2.8 cm long; sepals and petals green, streaked or suffused with reddish-brown; sepals elliptic-oblanceolate to oblanceolate, acute, thickened, concave above the middle, to 2.2 cm long, 8 mm wide; petals broadly obovate to spatulate, obtuse to acute, margin occasionally undulate-crisped, to 2.2 cm long, 6 mm wide; labellum adnate to base of column, deeply 3-lobed, to 1.8 mm wide, 1.9 mm long, light or dark purple, lateral lobes oblong to ovate-oblong, obtuse, clasping column, distally reflexed, midlobe separated from lateral lobes by a short isthmus, midlobe orbicular to obovate, apex subacute, margin undulate-crisped, upturned, callus is two keels diverging distally, passing into three low keels running nearly to apex, column

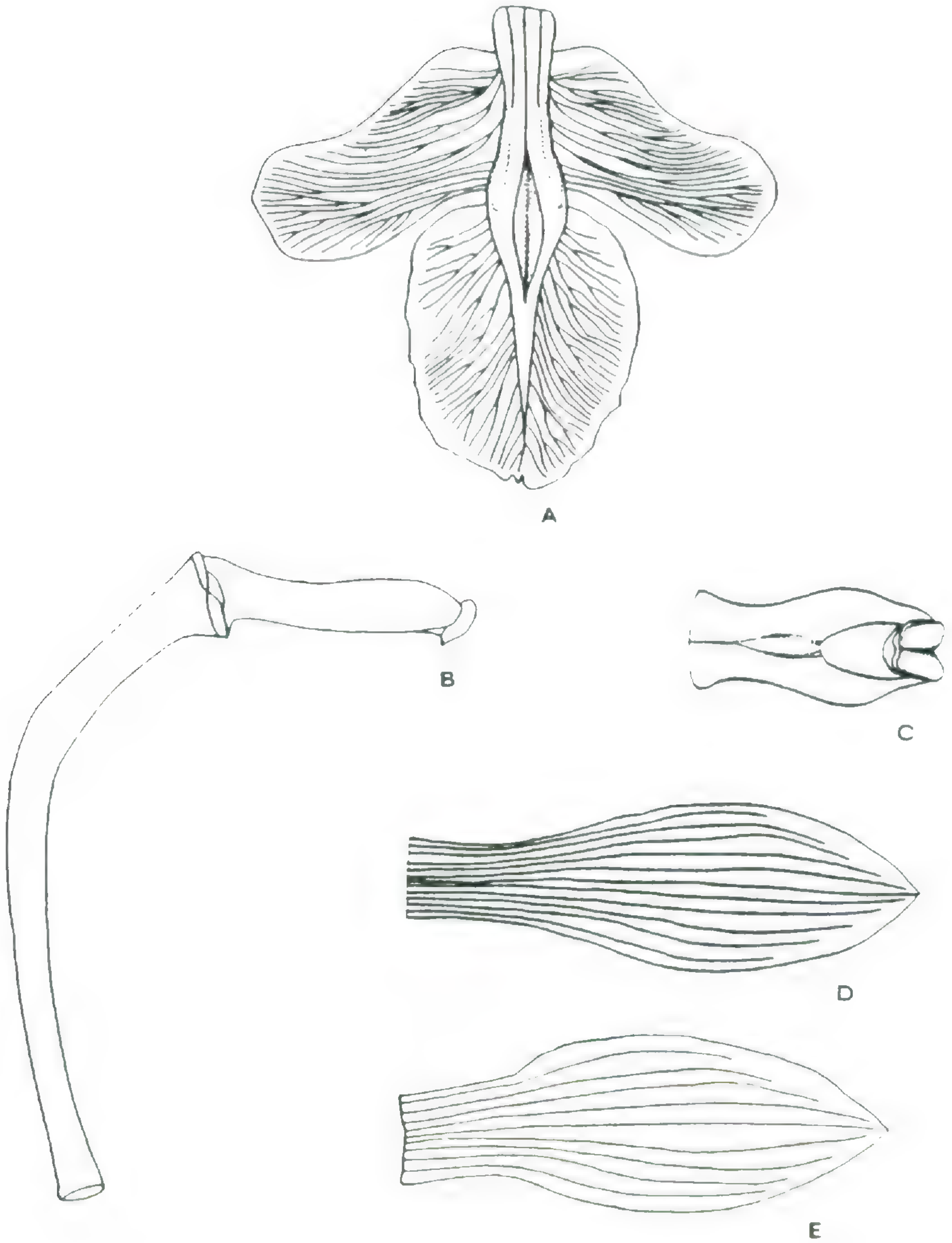

Figure 13. *Encyclia selligera* (Batem. ex Lindl.) Schltr. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

white with purple streaks, elongate, arcuate, to 1.3 cm long, 6 mm wide, lacking auricles, anther white; capsule pendent, to 3.5 cm long, 1.8 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Andros Island,** between Congo Town airport and Long Cay, along new road cut, 23 Sept. 1978, *Sauleda, Correll and Withner 2160* (FTG); 28 May 1979, *Sauleda 2547* (FAU), *2548* (FAU).

ADDITIONAL DISTRIBUTION: Reported by Ames and Correll (1952) from Chimaltenango, Guatemala and by Dressler and Pollard (1974) from Chiapas, Mexico.

REPRODUCTIVE PERIOD: May through July.

ECOLOGY: This rare species is found growing epiphytically on *Psidium longipes* (Berg) McVaugh in Low Coastal Coppices.

14. **Encyclia tampensis** (Lindl.) Small, Fl. Miami 56. 1913 (Fig. 14).

Basionym: *Epidendrum tampense* Lindl., Bot. Reg. **33:**Misc. 35. 1847. HOLOTYPE: Tampa Bay, Florida, *Torrey s.n.* (K L, photograph seen).

Epidendrum porphyrospilum Reichb. f., Linnaea **41**: 80. 1877. HOLOTYPE: Cultivated; from Florida, (W, photograph seen).

Plant epiphytic, rhizomatous, to 70 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, elliptic to ovate, attenuate, to 5 cm long, 3 cm wide, basally enclosed by scarious sheaths, to 2-leaved at apex; leaves coriaceous to rigid, linear-lanceolate, acute, to 28 cm long, 2 cm wide; inflorescence terminal, to 65 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 30 flowers; floral bracts ovate-triangular, acute, to 3 mm long, 4 mm wide; ovary pedicellate, slender, to 3.5 cm long; sepals green, yellow or ochraceous with reddish-brown suffusion, oblanceolate, acute, to 1.8 cm long, 4 mm wide; petals green, yellow or ochraceous with reddish-brown suffusion toward apex, spatulate, subobtuse to acute, to 1.5 cm long, 3 mm wide; labellum free, deeply 3-lobed, to 2.0 cm wide, 1.6 cm long, white with radiating purple lines on lateral lobes, midlobe with a central purple spot, lateral lobes oblong-ligulate, obtuse, erect, embracing column, midlobe round, emarginate to apiculate, callosity under column is two lateral erect keels joined by a third keel at junction of lobes and with two additional ridges on each side;

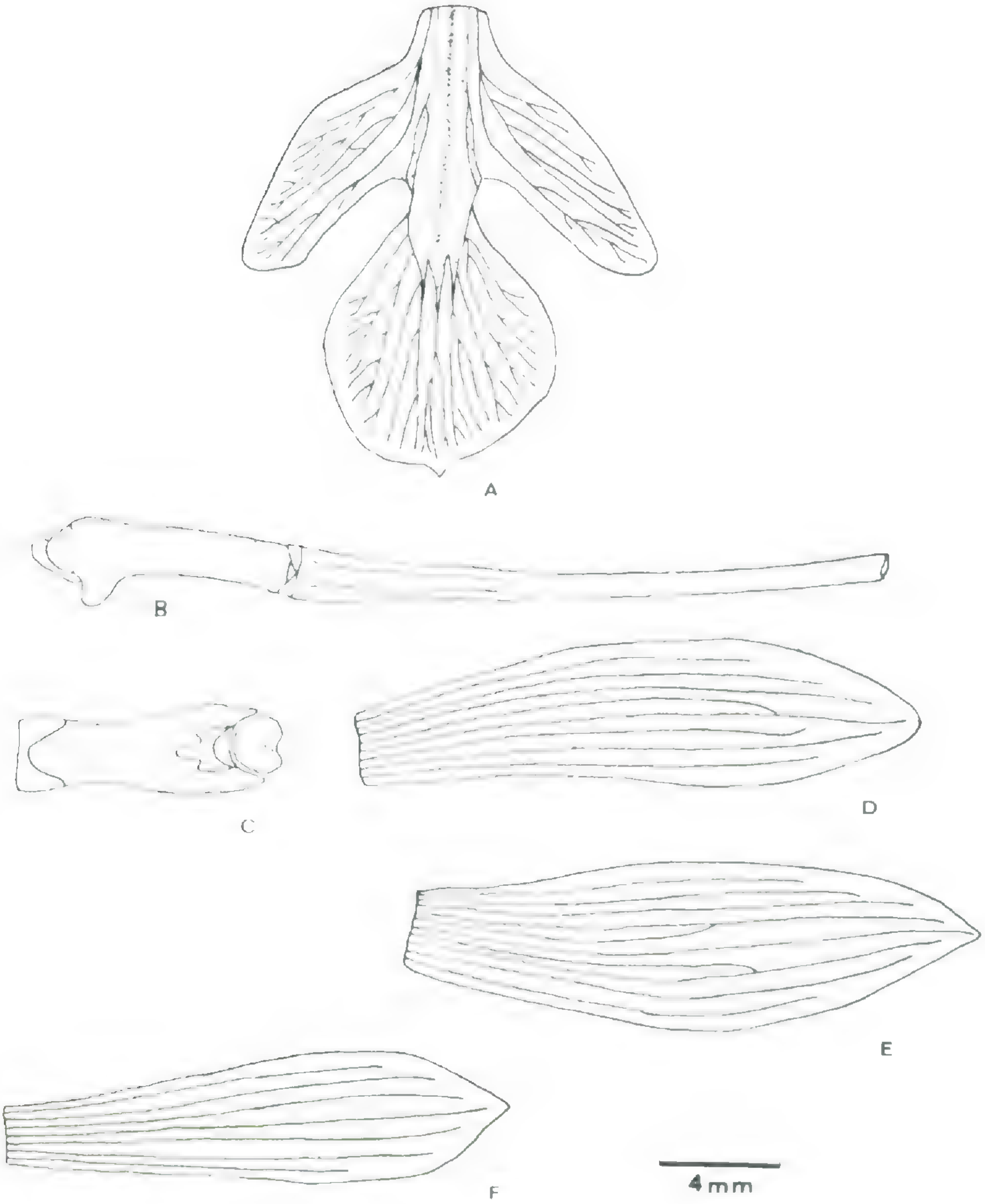

Figure 14. *Encyclia tampensis* (Lindl.) Small. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

column white, elongate, to 1.0 cm long, 4 mm wide, with membranaceous, incurved rounded auricles, anther yellow; capsules pendent, to 4.0 cm long, 1.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** low coppice, Abaco Heights, 2 Aug. 1979, *Sauleda, Adams and Adams 2762* (FAU). **Andros,** low coppice, Driggs Hill, 10 July 1976, *Sauleda 1008* (US), *1011* (NY), *1038* (AMES), *1047* (SEL), *1049* (FTG), *1061* (F).

ADDITIONAL DISTRIBUTION: **Florida,** *Brumbach 9014* (US).

REPRODUCTIVE PERIOD: May through July.

ECOLOGY: This species is found growing epiphytically on *Coccoloba diversifolia* Jacq. and *Acacia choriophylla* Benth. and grows in Low Coastal Coppices.

15. **Encyclia withneri** (Sauleda) Sauleda & Adams, Brittonia **33**(2): 187. 1981 (Fig. 15).

Basionym: *Epidendrum withneri* Sauleda, Amer. Orchid Soc. Bull. **46**(1): 34–35. 1977. TYPE: Andros, Bahama Islands, *Sauleda 1024* (HOLOTYPE: AMES; ISOTYPES: FAU, NY, USF).

Plant epiphytic, rhizomatous, to 70 cm tall; roots many, slender, velamentous; primary stem or rhizome short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect or ascending, clustered, ovate, to 5 cm long, 2 cm wide, basally enclosed by fugacious scarious sheaths, to 2-leaved at apex; leaves coriaceous, linear-oblong, acute, to 26 cm long, 1.5 cm wide; inflorescence terminal, to 65 cm tall, peduncles slender, erect, distantly several-sheathed, paniculate above, to 30 flowers; floral bracts ovate-triangular, obtuse to acute, to 3 mm long, 3 mm wide; ovary pedicellate, slender, muricate, to 2.3 cm long; sepals ochraceous with reddish-brown striping toward apex, dorsal sepal oblong to oblanceolate, acute, to 2.0 cm long, 5 mm wide, lateral sepals narrowly elliptic to oblanceolate, acute, to 1.8 cm long, 6 mm wide; petals ochraceous with reddish-brown striping toward apex, obovate to oblanceolate, acute, to 1.8 cm long, 5 mm wide; labellum 3-lobed, basal one-third adnate to column, to 1.6 cm long, 2.0 cm wide, white with radiating purple lines, lateral lobes oblong-ligulate, rounded, erect, apex recurved, midlobe round, bilobed, emarginate, margin undulate, callosity under column is two lateral erect keels with two additional ridges on each side, keels

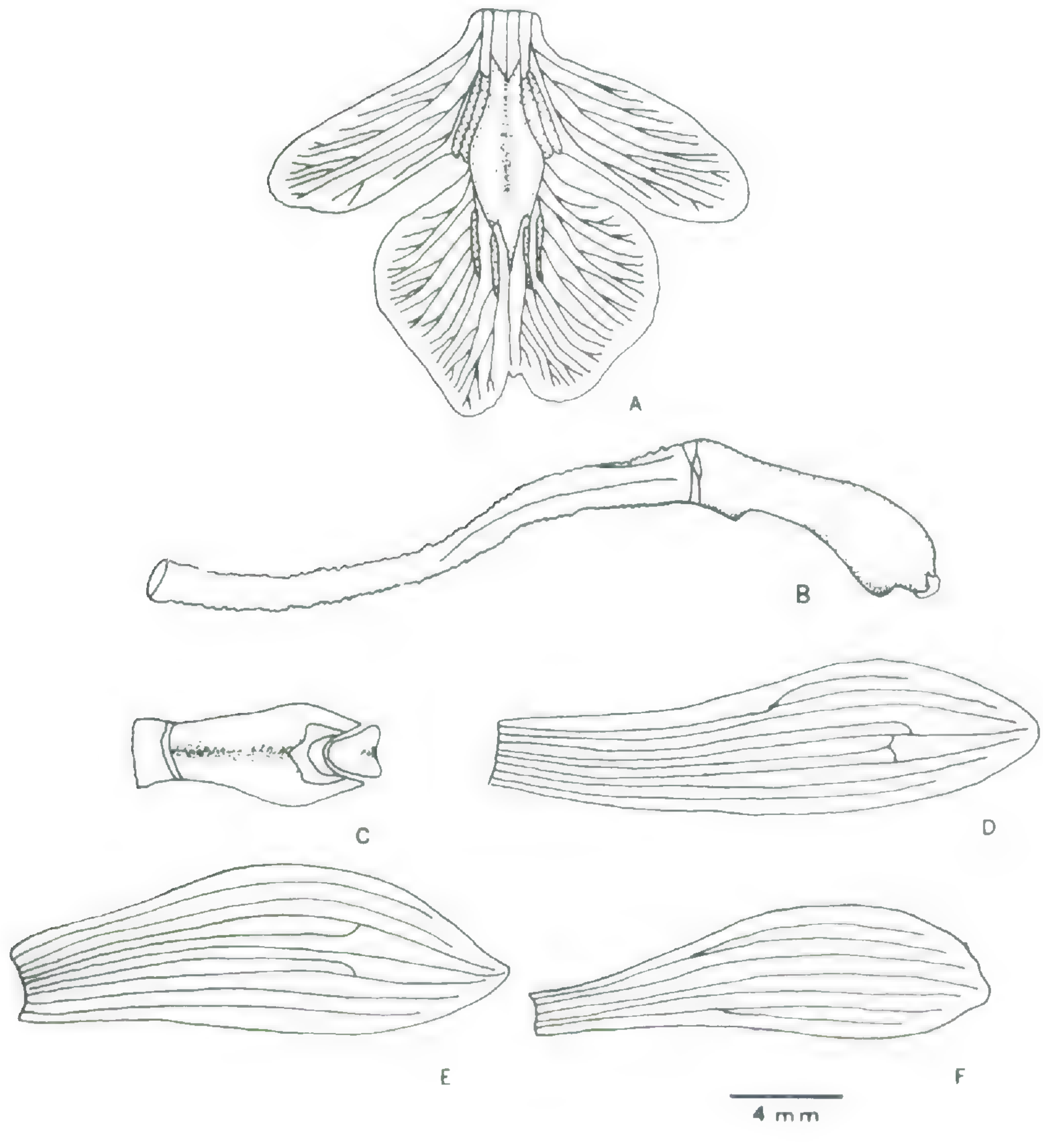

Figure 15. *Encyclia withneri* (Sauleda) Sauleda and Adams. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

terminate at junction of lobes with a fleshy, 3-dentate, plate-like callus, midlobe with five radiating, undulate, lamellae in front of callus; column white, elongate, to 1.0 cm long, 4 mm wide, with membranaceous, incurved, rounded auricles, anther yellow; capsules pendent, to 2.5 cm long, 1.5 cm thick.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Andros Island,** on trees in high coppice near Kemp's Bay, 21 June 1976, *Sauleda 1020* (FAU), *1023* (SEL), *1024* (AMES), *1025* (FTG).

REPRODUCTIVE PERIOD: May through June.

ECOLOGY: This species is found growing epiphytically on *Coccoloba diversifolia* Jacq. and *Acacia choriophylla* Benth. and grows in High Coppices. Endemic.

NATURAL HYBRIDS

16. **Encyclia** × **bajamarensis** Sauleda & Adams, Brittonia **33**(2): 189–190. 1981. (Fig. 16).

Encyclia gracilis (Lindl.) Schltr. ×*Encyclia rufa* (Lindl.) Britton & Millspaugh.

TYPE: Bahama Islands, Great Abaco, low coppice, Snake Cay Road, 27 May 1979, *Sauleda and Correll 2544* (HOLOTYPE: NY).

Plant predominatly epilithic, rarely epiphytic, rhizomatous, to 145 cm tall; roots, many, slender to thick, velamentous or canescent; primary stem short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect, clustered, elliptic-ovate to subulate, to 12 cm long, 7 cm thick, basally enclosed by scarious sheaths, to 4-leaved at apex; leaves coriaceous, stiff, linear to linear-lanceolate, acute, to 40 cm long, 3 cm wide, leaf bases lacking abscission layer; inflorescence, terminal to 133 cm tall, peduncles slender, erect, distantly sheathed, paniculate above, lateral branches semi-erect, to 60 flowers; floral bracts ovate-triangular, acute, concave, to 2 mm long, 1.8 mm wide; ovary pedicellate, slender, to 3 cm long; sepals, yellowish-orange with reddish-brown striping, obovate to oblanceolate, acute, to 2 cm long, 8 mm wide; petals, yellow-orange with reddish-brown striping towards apex, oblanceolate to spatulate, acute to obtuse, to 1.9 cm long, 6 mm wide; labellum free, deeply 3-lobed, to 2 cm wide, 2 cm long, yellow with radiating purple lines on lobes, lateral lobes oblong, obtuse to subacute, erect, embracing column, midlobe round to subovate, emarginate, margin usually undulate, callosity under column is two lateral erect keels joined by a third keel at junction of lobes; column white or yellow, occasionally streaked with purple, to 9 mm long, 4 mm wide, with membranaceous, incurved, rounded auricles, anther yellow or white.

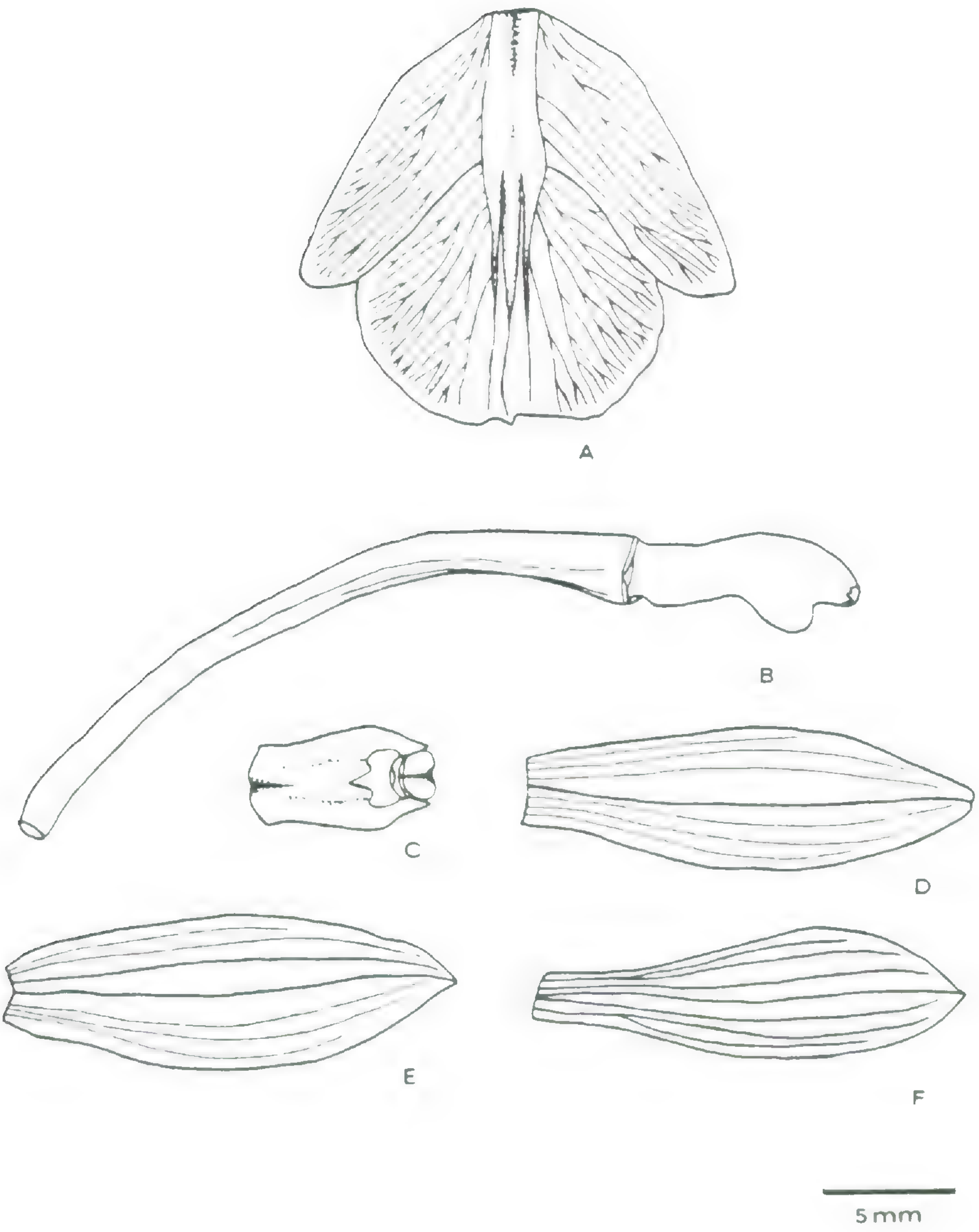

Figure 16. *Encyclia ×bajamarensis* Sauleda and Adams. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Great Abaco,** low coppice, Snake Cay road, 27 May 1979, *Sauleda and Correll 2544* (FAU). **Andros Island,** rock scrub, 8 mi S of Fresh Creek, 10 July 1976, *Sauleda 1067* (FTG); 15 Oct. 1976, *Sauleda 1148* (USF).

REPRODUCTIVE PERIOD: May through July.

ECOLOGY: This natural hybrid is found growing epilithically on Pleistocene limestone and occasionally epiphytically at the base of *Psidium longipes* (Berg) McVaugh. The habitats in which it is found are Coastal Rock Scrub and Low Coastal Coppice. Endemic.

17. **Encyclia** × **lucayana** Sauleda and Adams, Brittonia **33**(2): 190–191. 1981 (Fig. 17).

Encyclia gracilis (Lindl.) Schltr. ×*Encyclia fehlingii* (Sauleda) Sauleda & Adams

TYPE: Bahama Islands, Great Abaco, low coppice, Snake Cay road, 2 Aug. 1979, *Sauleda, Adams and Adams 2776* (HOLOTYPE: NY; ISOTYPES: US, USF).

Plant predominantly epilithic, rarely epiphytic, rhizomatous to 136 cm tall; roots many, slender to thick, velamentous to canescent; primary stem short, stout, creeping or ascending, enclosed by imbricating scarious sheaths; secondary stems modified into pseudobulbs, erect, clustered, elliptic-ovate to subulate, to 9 cm long, 4 cm thick, basally enclosed by scarious sheaths, to 4-leaved at apex; leaves coriaceous, linear to linear-lanceolate, acute, to 47 cm long, 2.5 cm wide, leaf bases lacking abscission layer; inflorescence terminal, to 127 cm tall, peduncles slender, erect, distantly sheathed, paniculate above, to 60 flowers; floral bracts ovate-triangular, acute, concave, to 1.5 mm long, 1.5 mm wide; ovary pedicellate, slender, to 3 cm long; sepals and petals green to yellowish-orange, usually with reddish-brown striping; sepals elliptic to oblanceolate, acute, to 2 cm long, 5 mm wide; petals oblanceolate to spatulate, acute, to 1.8 cm long, 4 mm wide; labellum free, deeply 3-lobed, to 1.9 cm long, 1.9 cm wide, white with radiating purple lines on lobes, lateral lobes oblong, obtuse to subacute, erect, usually embracing column, midlobe round, emarginate, margin usually undulate, callosity under column is two lateral erect keels joined by a third keel at junction of lobes and extending on to disc; column to 10 mm long, 5 mm wide, white, occasionally with purple streaks, with membranaceous incurved rounded auricles, anther yellow or white.

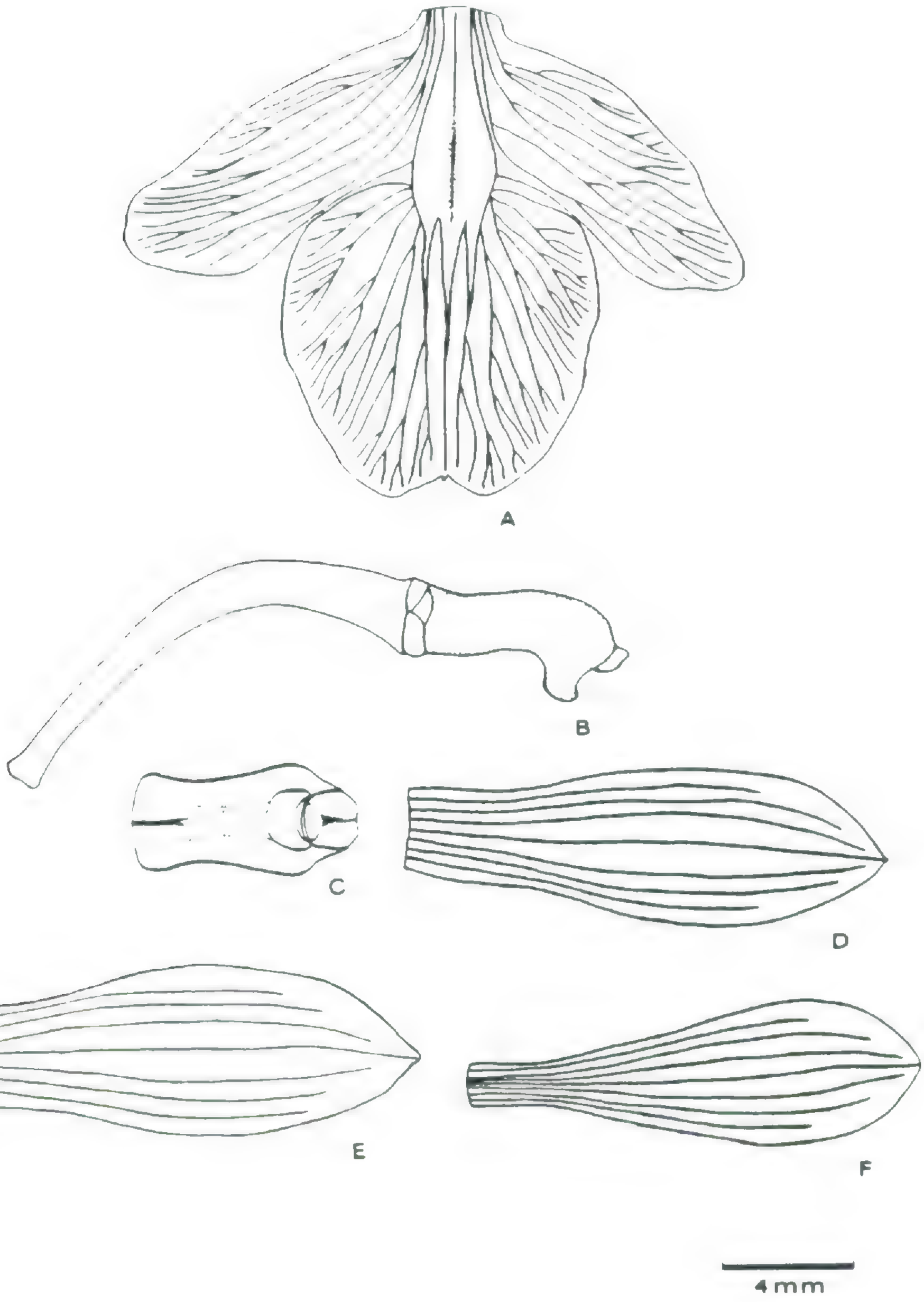

Figure 17. *Encyclia ×lucayana* Sauleda and Adams. **A**. Labellum, frontal view; **B**. Column and ovary, lateral view; **C**. Column, ventral view; **D**. Dorsal sepal; **E**. Lateral sepal; **F**. Petal.

DISTRIBUTION IN THE BAHAMA ISLANDS: **Andros Island,** low coppice, 3 mi S of Stafford Creek, 8 Oct. 1977, *Sauleda 1976* (USF, FAU). **Great Abaco,** high coppice, 3 mi NW of Dundas Town, 2 Aug. 1979, *Sauleda, Adams and Adams 2734* (US); low coppice, snake Cay road, 2 Aug. 1979, *Sauleda, Adams and Adams 2776* (NY, US, USF)., *2777* (FTG), *2778* (USF), *2779* (FAU); low coppice, Cherokee Sound, 3 Aug. 1979, *Sauleda 2868* (FAU).

REPRODUCTIVE PERIOD: July through August.

ECOLOGY: This natural hybrid is found growing epilithically on Pleistocene limestone or epiphytically on *Psidium longipes* (Berg) McVaugh, *Coccoloba diversifolia* Jacq., and *Ateramnus lucidus* (Sw.) Rothm. The habitats in which it is found are Low Coastal Coppice and at the periphery of High Coppices. Endemic.

ACKNOWLEDGMENTS

We wish to thank the directors, curators and staff members of the herbaria previously mentioned for their cooperation. We acknowledge the generous field assistance given by Patricia H. Adams, Dr. Donovan S. Correll, Diane K. Sauleda, and Kenneth and Gladys Fehling. This research was supported in part by donations and grants from the Tropical Orchid Society, the Dallas Ft. Worth Orchid Workshop, the Florida Caribbean Orchid Association, the Delray Beach Orchid Society, the Ft. Lauderdale Orchid Society, and the American Orchid Society.

LITERATURE CITED

ADAMS, R. M., R. P. SAULEDA, & B. C. BENNETT. 1982. The Orchidaceae of the Bahama Archipelago—Taxomony, Ecology and Biogeographic Patterns. *In*: Proceedings of the 10th World Orchid Conference, Durban, South Africa, Eds. J. Steward and C. N. van der Merwe.

AMES, OAKES, & DONOVAN S. CORRELL. 1952. Orchids of Guatemala. Fieldiana Bot. **26**:1–395.

CORRELL, D. S., & H. B. CORRELL. 1982. Flora of the Bahama Archipelago (Including the Turks and Caicos Islands). J. Cramer, Vaduz, Leichtenstein.

DRESSLER, R. L. 1961. A reconsideration of *Encyclia* (Orchidaceae). Brittonia **13**: 253–266.

_____, & GLENN E. POLLARD. 1974. The Genus *Encyclia* in Mexico. Assoc. Mex. de Orq., A.C., Mexico, D.F.

HOOKER, W. J. 1828. *Encyclia viridiflora* Hook. Curtis's Botanical Magazine II, pl. 2831.

PABST, G. F., J. L. MOUTINHO, & A. V. PINTO. 1981. An attempt to establish the right statement for Genus Anacheilium Hoffmgg. and revision of the genus Hormidium Lindl. ex Heynh. Bradea 3(23): 173–186.

SAULEDA, RUBEN P., & RALPH M. ADAMS. 1979. The Epiphytic Orchids of Andros. The Bahama Naturalist 4(2): 25–33.

SCHLECTER, R. 1915. Die Orchideen. Paul Parey, Berlin.

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TAXONOMIC TREATMENT OF THE *CHAETOMORPHA* AND *RHIZOCLONIUM* SPECIES (CLADOPHORALES; CHLOROPHYTA) IN NEW ENGLAND[1]

Stephen M. Blair[2]

ABSTRACT

A key to the species of *Chaetomorpha* and *Rhizoclonium* found in New England is presented along with a description and review of each species' ecology, distribution, and taxonomic history. *Chaetomorpha picquotiana* is shown to be an earlier name for *C. atrovirens*, and discussions concerning the generic placement of *Chaetomorpha cannabina* and the separation of the genera *Chaetomorpha* and *Rhizoclonium* are presented.

The genera *Chaetomorpha* Kützing (1845) and *Rhizoclonium* Kützing (1843) have posed numerous taxonomic problems for phycologists. The reasons for these problems appear multifold. A general lack of understanding of the phenotypic variability of species at the time of their description, a small number of characters of taxonomic significance, and varied interpretations of morphological circumscription have resulted in the recognition of ill-defined species within these genera.

In attempting to resolve this confusion, it is essential to determine the reliability of as many characters as possible. Unfortunately a number of characters used in the past are dependent on plant maturity (number of nuclei per cell, cell wall thickness and stratification, pyrenoid number, reproductive patterns) and on environmental conditions (color, state of attachment, rhizoid number and complexity). The suitability of application of such characters should, therefore, be evaluated on a species-by-species basis. At present, evaluation of morphological variability remains the major basis for species circumscription.

A previous report (Blair, et al., 1982) described the electrophoretic and morphological patterns and specific separation of

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Chaetomorpha linum (Müll.) Küt., *C. aerea* (Dillw.) Küt., *C. picquotiana* Montagne ex Kützing (as *C. atrovirens* Taylor) and *C. melagonium* (Web. et Mohr) Küt. based on a morphological and biochemical analysis of the species *Chaetomorpha* and *Rhizoclonium* in New England (Blair, 1978). The present report summarizes the morphological findings of the latter report through presentation of artificial keys and descriptions of the species, and reviews the ecology, distribution, and taxonomic history of each species. Acronyms for herbaria follow those of Holmgren and Keuken (1974).

KEY TO THE SPECIES OF CHAETOMORPHA AND RHIZOCLONIUM IN NEW ENGLAND

1. Filaments uniseriate, attached by a single basal cell, or unattached and greater than 75 μm diam. ..... *Chaetomorpha* p. 176.
1. Filaments unattached, with or without rhizoids, and less than 75 μm diam. ..... *Rhizoclonium* p. 197.

CHAETOMORPHA

Chaetomorpha Kützing (1845) Phyco. Germ p. 203 (nom. cons.)

TYPE: *Chaetomorpha melagonium* (Web. & Mohr) Kützing. (1845) Phyco. Germ. p. 204
Type locality; North Sea

Chloronitum Gail. et Levrault (1828) Dict. Sci. Not. Vol. **LIII** p. 389-390.
Spongopsis Kützing (1843) Phyco. Gen. p. 261.
Aplonema Hassel (1845) Brit. Fresh. Alg. p. 213.

The genus *Chaetomorpha* contains species of uniseriate unbranched filaments with multinucleated cells, and a single reticulate parietal chloroplast containing numerous pyrenoids. Attachment is by a discoid holdfast cell (basal cell) which may produce "haptera-like" projections capable of "budding" off new plants. All of the species have an attached stage at some period in their life history. Some species become detached and remain in drift for the major part of their life span. Unattached species often become entangled among coarse algae and are capable of forming extensive masses. All of the species investigated thus far exhibit an isomorphic alter-

nation of generations by isogamous biflagellate gametes and quadriflagellate zoospores. Some species may recycle the same generation via bi- or quadriflagellate zoospores.

Taxonomic History

The genus *Chaetomorpha*, established by Kützing in 1845, was predated by Kützing's *Spongopsis* (Kützing, 1843) and Gaillon's (1828) *Chloronitum*. Due to the general acceptance of the name *Chaetomorpha*, Silva (1950) proposed that it be conserved. The proposal was accepted and listed under "Generica Conservada" in the International Code of Botanical Nomenclature (Stafleu, 1956).

KEY TO THE NEW ENGLAND SPECIES OF CHAETOMORPHA

1. Filaments attached by a basal cell ..... 2.
2. Filaments less than 75 μm diam., epiphytic on coarse algae ..... *C. minima* p. 195.
2. Filaments greater than 75 μm diam. ..... 3.
3. Filaments erect, straight, 350 to 850 (<1000) μm wide, with basal cell length/width ratio (LWR) of 10 to 12, plants of sublittoral or low intertidal pools ..... *C. melagonium* p. 190.
3. Filaments less than 350 μm wide, curled or having basal cell LWR of less than 8 ..... 4.
4. Basal cell much longer than cells of the upper portion of the filament ..... 5.
5. Filaments curled, cells 175–450 μm diam., basal cell LWR less than 5, plants of mid-littoral or sublittoral region ..... *C. linum* p. 178.
5. Filaments straight, cells 125–400 μm diam., basal cell LWR to 10, plants of mid and high littoral pools ..... *C. aerea* p. 187.
4. Basal cell not longer than cells of the upper filament ..... 6.
6. Cells 200–400 μm diam., curled, mean cell LWR 2.0–5.0 ..... *C. piquotiana* p. 181
6. Cells 75–150 μm diam., curled or straight, mean cell LWR 0.75–3.0 ..... *C. brachygona* p. 192.
1. Filaments unattached, though often intricately entangled among coarse algae ..... 7.

7. Cells 75–150 μm diam., mean cell LWR 0.75–3.0 .... *C. brachygona* p. 192.
7. Cells 150–450 μm diam., mean cell LWR 0.75–1.5 or 2.0–5.0 ..... 8.
8. Filaments curled, cells 150–450 μm diam., usually light green, mean cell LWR 0.75–1.5..... *C. linum* p. 178.
8. Filaments curled, cells 200–400 μm diam., usually dark green, mean cell LWR 2.0–5.0... *C. piquotiana* p. 181.

Chaetomorpha linum (Müller) Kützing (1845) Phyco. Germ. p. 204

Basionym: *Conferva linum* Müller (1778) Flora Danica. 5(13)

TYPE: *Conferva linum* Müller (1778) Flora Danica. 5(13) t. 771 f. 2

Type locality: Nakskov Fjord and Rodby Fjord, Denmark.

Conferva capillaris L. 1753. Sps. Plant. 2:1166.

Chaetomorpha chlorotica (Mont.) Kütz. 1849. Sps. Alg., p. 377; 1853. Tab. Phyc., III, t. 54, f. 1

Chaetomorpha brachyartha Kütz. 1853. Tab. Phyco. t. 53, f. 4.

Conferva brachyartha Kütz. 1843. Phyco. Gen. p. 206.

Conferva capillaris Dillw. 1806. Brit. Conf. t. 9, p. 46.

Chaetomorpha dalmantic Küt. 1845. Phyco. Germ. t. 203; 1853. Tab. Phyc. III t. 57, f. 1.

Chaetomorpha setacea (Ag.) Küt. 1849. Sps. Alg. p. 378; 1853. Tab. Phyc. III t. 4, f. 1.

Conferva setacea C. Ag. 1824. Sys. Alg. p. 98.

Chaetomorpha urbica (Zand.) Küt. 1847. Bot. Zietg. V:168; 1853. Tab. Phyc. III t. 54, f. 3.

Chaetomorpha aerea (Dillw.) Küt. f. *linum* (Müll.) Collins 1909. Grn. Agl. of N. Amer. p. 325.

The plants (Fig. 1) are usually found entangled and unattached among coarse algae, rarely found attached (initially) by a single basal cell. The plants are stiff, not collapsing on removal from water, the cells are cylindrical to barrel shaped with a diameter of 150 450 μm and a LWR (length width ratio) of 0.75 to 1.5 (Fig. 2a). The basal cell, when present, is 3 to 8 times longer than broad. Gametes are reported from April to August, zoospores from August to November (Taylor, 1957), though no fertile material was found in specimens examined.

Distribution and Ecology

The species shows a world-wide distribution, extending from

Figures 1 and 2. Fig. **1,** Habit of *Chaetomorpha linum.* Fig. **2,** comparative cell sizes of *C. linum* and *C. picquotiana. 2a — C. linum,* 2b — *C. picquotiana* (Scale = 100 μm).

Panama to Labrador, South Africa to Norway, Australia to Japan and California to Alaska. In New Hampshire it occurs in coastal and estuarine areas with decreasing abundance in inner estuarine locales where salinities are less than 10 ppt. It grows within the littoral zone, entangled among coarse algae and in tide pools, as well as to −18 m below MLW. In estuarine tidal rapids this species may form estensive masses (skeins) up to 3 m in length and 0.5 m diam. Kornmann (1972) and Patel (1972) have induced sporulation and gametogenesis in culture but they give no records of in situ reproductive phenology.

Representative Specimens:

Africa. Comerunia Jungner, Wittrock & Nordstedt Algae Exsic. 1049 (UC). **Australia.** Coffin Bay: *Womersly A31820* (UC). **Bermuda.** Hamilton Harbor; *Collins s.n.* 5 March 1913 (UC). Faryland; *Collins 311* (FH). **Canada.** NEWFOUNDLAND: Alexander Bay, *Hooper & Roberge 10144* (NFLD); Placentia Bay, *Whittick & Hooper 8393* (NFLD). NOVA SCOTIA: Dunns Beach, *South and Whittick 6751* (NFLD). **Chile.** Valparaiso, Montinom, *Etchenerry s.n.*, 1951, (UC). **France.** Cherbourg: LeJolis, Algeres Marines de Cherbourg 258 (UC). Banyuls, *Feldman 1726* (UC). **Holland.** Nievnedup, Weber-Von Bose, Hauk et Richter Phyco. Univ. 125, & 468, (UC). **India.** *Wright s.n.*, (FH). **Italy.** Isola di Caprera, Levi-Monenas, Phyco. Italica 185 (UC). **Japan.** Enoshima, Kamara, K. 9 Alg. Japanica Exsic. 93 (UC). **Panama.** Caledonia Harbor: *Taylor 39–183* (UC, FH). **Philippines.** Guanica Harbor: Howe, N. Amer. Marine Algae 7035 (FH, UC). **Sweden.** Bhausia Maj: Areschoug, Alg. Scand. Exsic. Fasc. secundus 134 (UC). **Tahiti.** Society Island: Tilden, South Pacific Algae 21 (UC).

United States. ALASKA: Tangas Is., *Lichentater 1887* (FH). CALIFORNIA: Santa Clara Co., San Martin Is., *Howe 201* (UC). MAINE: York Co., Kittery, Malaga Is., *Mathieson s.n.*, 16 April 1976 (NHA). Seapoint, *Blair s.n.*, 2 October 1977 (NHA). MASSACHUSETTS: Barnstable Co., Woods Hole, *Doty 6722* (FH). Buzzard's Bay, *Taylor s.n.*, 2 August 1944 (NFLD). Gloucester, Farlow Algae Exsic. Am.-Bor. 175 (FH). Salem, Hauk, Collins Et Richter Phyco. Univ. 469 (FH). NEW HAMPSHIRE: Rockingham Co., Dover, *Mathieson s.n.*, 21 October 1977 (NHA). *Mathieson s.n.*, 3 August 1976 (NHA). Newington, *Conway et. al. s.n.*, 6 July 1966 (NHA). Portsmouth, *Conway & Hehre s.n.*, 20 April 1966 (NHA). Durham, Adam's Point, *Mathieson s.n.*, 30 December 1973 (NHA). NEW JERSEY: Monmouth Co., *Maul s.n.*, 17 October 1956 (UC). OREGON: Coos Co., *Chadwick 907* (UC). RHODE ISLAND: Newport Co., Newport, *Clark s.n.*, July 1890 (FH).

Yucatan: Campeche Bank, *Connover & Perkins s.n.*, 15 July 1960 (NHA).

Taxonomic History

Chaetomorpha linum was described in Species Plantarum (Linnaeus, 1753) under the name *Conferva capillaris*. The filaments were described as being simple, with joints alternately compressing on drying. Müller's (1778) original description of *Conferva linum* was very similar to *C. capillaris* L. Subsequently, Roth (1797) gave

separate descriptions of *C. linum* and *C. capillaris*. It is apparent that the name *C. linum* has been maintained due to its more detailed description. Børgesen (1925) noted the nomenclatural confusion between *Conferva capillaris* and *C. linum* and proposed the acceptance of *C. linum* over *C. capillaris* due to its long usage and entrenchment. However, the International Code of Botanical Nomenclature (Stafleu, 1978) has no provision for the conservation of species names.

It should be noted that the transfer of *Conferva capillaris* L. to *Chaetomorpha* would create a homonym with *C. capillaris* (Kützing) Børgesen, contrary to Article 55, of the International Code of Botanical Nomenclature (Stafleu, 1978). Thus, the next validly published name, *Conferva linum* Müller, may be applied to the taxon. *Conferva linum* Müller was transferred to *Chaetomorpha* by Kützing (1849); as a result *Chaetomorpha linum* (Müller) Kützing is the correct name, with *C. capillaris* L. being placed into synonymy. The confusion between *C. linum* and *C. aerea* is discussed in the taxonomic history section under *C. aerea*.

Chaetomorpha picquotiana Montagne ex Kützing 1849. Species Algarum p. 379

Basionym: *Conferva picquotiana* Montagne. 1849. Ann. Sci. Nat. 3d Ser. **11:** 66.

LECTOTYPE?: *Conferva picquotiana* Lamare-Picquot s.n. (PC) in (FH)

Type locality: Labrador

Chaetomorpha melagonium f. *typica* Kjellman sensu Collins 1909. Green Alg. of N. America. p. 323.

Chaetomorpha atrovirens Taylor. 1937. Pap. Mich. Acad. Sci. Arts. Lett. **22:** 227–8.

The species forms entangled masses in littoral pools as well as among coarse algae in the littoral and sublittoral zones (Fig. 3). The cells range from 225–400 μm in diameter with LWR's of 2–8 (Fig. 2b). Juvenile attached filaments have an attenuated basal cell (Fig. 4) which is similar in diameter to the upper cells of the filament. The discoid holdfast cell may form non-septate rhizoidal projections. The species is distinguished from *Chaetomorpha linum* by its larger LWR, *C. picquotiana* being greater than 2.0 while *C. linum* is less than 1.5 (Blair, et al., 1982). The plant reproduces by vegetative

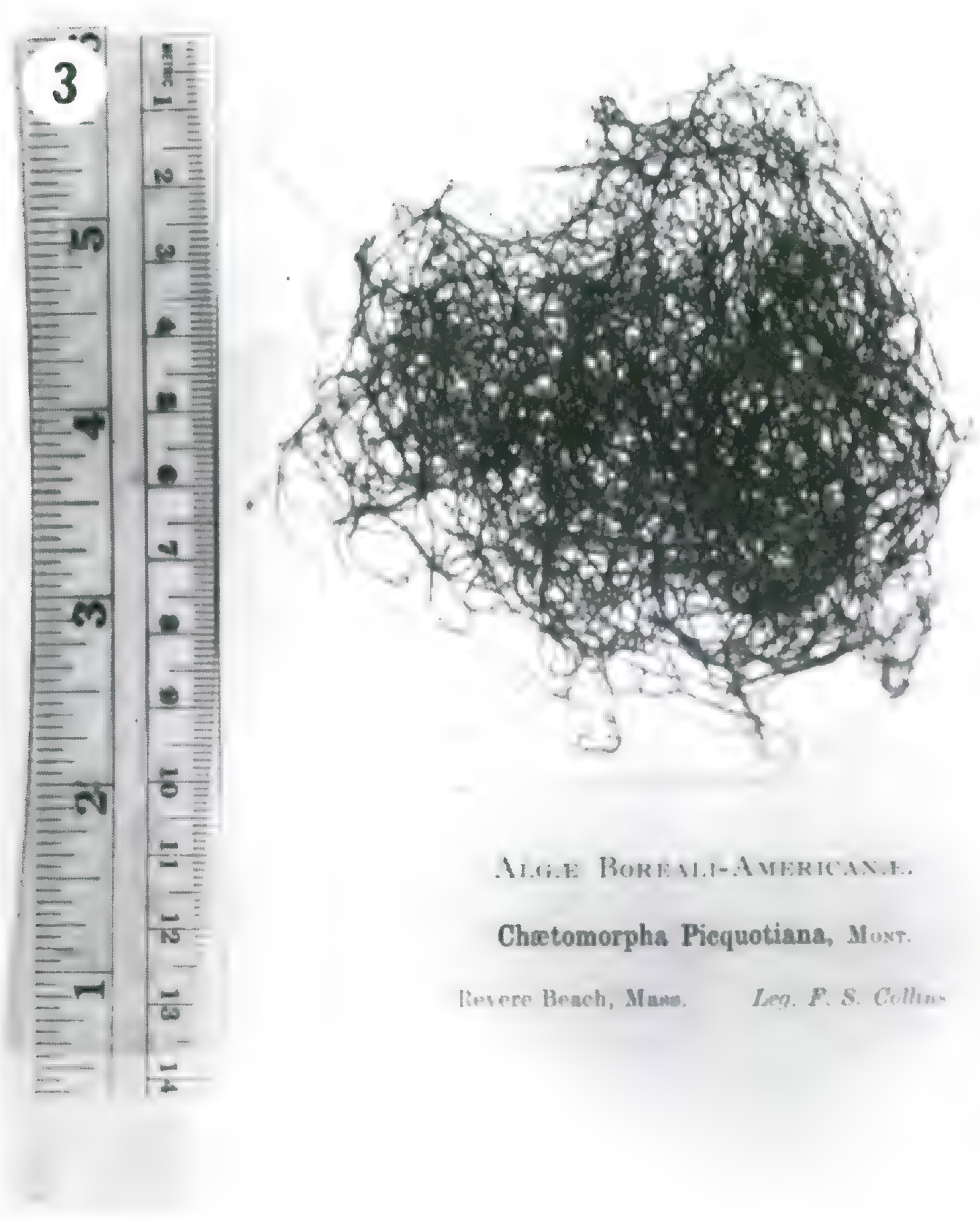


Figure 3. Habit of *Chaetomorpha picquotiana*.

propagation (i.e., fragmentation). An isomorphic alternation of generations is assumed to occur.

Distribution and Ecology

Chaetomorpha picquotiana has its major center of distribution in northern North America, north of Long Island on the east coast, and from Oregon northwards on the west coast. However, a few records of *C. picquotiana* have been confirmed from Florida and Bermuda. The species distribution is very similar to that of *C. melagonium* with which it may be closely related (Blair, et al., 1982).

Chaetomorpha picquotiana shows a broad distribution within the Great Bay estuary, New Hampshire, except at the headwaters of riverine habitats where salinities are less than 10 ppt.

Representative specimens:

Bermuda. Hamilton Islands: *Bernatowicz 49-624* (UC), *Hamilton GRO 2807* (NFLD). **Canada.** BRITISH COLUMBIA, Henderson Point, *Hooper s.n.*, 2 January 1971 (NFLD). LABRADOR. *Lamare-Picquot s.n.* (PC) in (FH). NEWFOUNDLAND. Little Bay Est., *South, Whittick 413* (NFLD); Salmonier, *Mathieson 9d* (NFLD); Placentia Bay, *Hooper & Reddin 12495* (NFLD). NOVA SCOTIA. Muder Island, *Hooper 15264* (NFLD). PRINCE EDWARD ISLAND. *Macon s.n.*, 29 June 1888 (FH).

United States. ALASKA. Unalaska, *Womersley 1848* (FH). FLORIDA. Monroe Co., Key West, *Curtis s.n.*, August 1895 (FH). MAINE. Cumberland Co., South Harpswell, *Tyler & Brannigan s.n.*, 4 March 1966 (NHA). Knox Co., Rockland, *Clarke s.n.*, 3 December 1895 (NFLD). York Co., Kittery, *Mathieson s.n.*, 16 June 1966 (NHA), *Blair s.n.*, 6 December 1977 (NHA). MASSACHUSETTS. Barnstable Co., Great Brewster Is., *Hutchinson s.n.*, 20 October 1971 (NHA). Salem, *Femino s.n.*, 4 August 1966 (NHA). Gloucester, *Farlow s.n.*, September 1878 (FH). Revere Beach, *Collins s.n.*, 12 April 1884 (FH). Swampscott, *Collins s.n.*, (FH). NEW HAMPSHIRE. Rockingham Co., Hampton, *Mathieson s.n.*, 19 April 1966 (NHA). Seabrook, *Hutchinson B431* (NHA), *Searles* s.n., 7 March 1966 (NHA). Portsmouth, *Cheney & Kilar s.n.*, 27 February 1976 (NHA). Newcastle, *Voorhees & Mathieson s.n.*, 24 July 1976 (NHA). Strafford Co., Dover, *Mathieson s.n.*, 20 April 1977 (NHA). RHODE ISLAND. Newport Co., *Kingston s.n.*, (NHA).

Taxonomic History

The species was described by Montagne (1849) as *Conferva picquotiana*. Kützing (1849) published *Chaetomorpha picquotiana* attributing it to Montagne, "in litt.". Therefore as suggested by P. C. Silva (pers. comm.) the authorization of *Chaetomorpha picquotiana* is best attributed to Montagne ex Kützing. Much of the confusion concerning this taxon's proper specific designation centered around the fact that the species was described as being attached. This, in combination with the length of the cells, has led authors to speculate that *C. picquotiana* and *C. melagonium* were conspecific, and that a long celled unattached species, *C. atrovirens* Taylor (1937) was simply a detached phase of the attached plant. Harvey (1857) was the first to express an opinion on the relationship between *C. picquotiana* and *C. melagonium*. He compared Montagne's material with *Chaetomorpha melagonium* and concluded the two were separate species but noted that *C. picquotiana* "is nearly related to *C. melagonium*, but of larger dimensions and with much longer articulations". It should be noted that Harvey was

Figure 4. Basal holdfast cell of a *C. picquotiana* filament (Scale = 100 μm).

applying the name *C. picquotiana* to the detached, entangled entity (*C. atrovirens* sensu Taylor) and had not found the species attached. Farlow (1881), also referring to unattached material, stated that it was "probable" that "it is merely an advanced stage" of *C. melagonium* that had broken off. Kjellman (1889) placed *C. picquotiana* under *Chaetomorpha melagonium* f. *typica* Kjellm. Kjellman cited Kützing's illustration of *C. picquotiana* (Kützing, 1853), Weber and Mohr's description of *C. melagonium* (Weber & Mohr, 1804) and Wittrock and Nordstedt's specimen of *C. melagonium* (Witt. and Nords. Alg. Exsicc. 1877-87 #415). As no explanation of the synonymy was given it may only be speculated that similarities in the original descriptions led Kjellman to place *C. picquotiana* into synonomy. Unfortunately, Kjellman did not state whether the *C. picquotiana* of Harvey and Farlow (unattached material) should be included with it. Collins (1909) carried forth the classification of Kjellman and the interpretation of Harvey and Farlow, referring to the unattached material as *C. melagonium* f. *typica*. Collins noted that the unattached material had previously been known as *C. picquotiana* "but is now pretty generally recognized as a form of the present species." Setchell and Gardner (1920) discussed the varied usage of *C. picquotiana* and *C. melagonium* f. *typica*. They felt that due to the similarity of the original descriptions of the plants, that Kjellman's placement of *C. picquotiana* under *C. melagonium* may be proper. Further, they questioned whether unattached material found in New England had been properly designated as *C. picquotiana*, for if, as Harvey and Farlow believed, it was simply a detached phase of the attached material, then such a "phase" would be present on the Pacific Coast in the regions where *C. melagonium* occurs. The apparent absence of the phase on the northwest coast led them to discount the application of *C. picquotiana* to the unattached material in New England. Taylor (1937) proposed the name *Chaetomorpha atrovirens* for the unattached, entangled New England species. Taylor discounted the previous designations of the taxon as *C. melagonium* f. *typica* on the basis of a lack of "any convincing demonstration" of a relationship between *C. melagonium* and the unattached plant, and cited the objections of Setchell and Gardner to the use of *C. picquotiana*. It should be noted that of the above authors only Harvey examined original material of *C. picquotiana*.

Thus, *Chaetomorpha picquotiana* has remained in synonomy

under *Chaetomorpha melagonium* and the unattached material has been referred to as *C. atrovirens*. Through the courtesy of the National Museum of Natural History, Paris (PC) and the Farlow Herbarium of Harvard University, Cambridge (FH), original specimens of *Conferva picquotiana* from Montagne's herbarium were examined. The specimens bore little resemblance to *C. melagonium*. The cells of the *C. picquotiana* filaments ranged in length from 609 to 1551 μm (mean = 963) and in width from 250 to 325 μm (mean = 284.5). The length/ width ratios ranged between 2.1 and 5.4 (mean = 3.4). The above dimensions are well within the cell ranges shown by Blair, et al. (1982) for populations of *C. atrovirens*. The cells of *C. picquotiana* did not show an increase in length toward either end of the filament. The filaments showed much greater length/ width ratios in the upper portions of the filament and longer and shorter cells were apparently randomly situated within the filament, as compared to a decrease in LWRs seen in the upper portion of *C. melagonium* filaments. The overall habit of the *C. picquotiana* specimens was indistinguishable from samples of *C. atrovirens* distributed in Collins' Phyco. Bor.-Amer. and those on deposit in the Herbarium of the University of Michigan, Ann Arbor (MICH) and in W. R. Taylor's herbarium.

As stated before, the apparent reason for indecision on the classification of this plant was the reference to the basal attachment in the original description. It should be noted that none of the original material examined, nor the illustrations (Kützing 1853; Harvey 1857), showed any holdfast or attachment cell. As seen in Fig. 4, the unattached New England material may initially be attached, by a modestly differentiated basal cell. The lack of an indication of attachment other than the basal cell itself means that if the lower portion of the holdfast cell were broken off during collection, all signs of attachment would be destroyed. This could account for the reference to basal attachment in the original description and absence of any signs of holdfasts on the original samples.

Thus, on the basis of the overall dissimilarity of *Chaetomorpha picquotiana* with *C. melagonium*, *C. picquotiana* should be removed from synonymy with *C. melagonium*. Further, due to the morphological inseparability of original specimens of *C. picquotiana* and *C. atrovirens* and for reasons stated above, it is apparent that *C. picquotiana* and *C. atrovirens* are conspecific. *Chaetomorpha picquo-*

tiana is the earlier name and *C. atrovirens* Taylor should be placed into synonymy under *C. picquotiana*.

Chaetomorpha aerea (Dillwyn) Kützing. 1849. Species Algarum p. 379–380.

Basionym: *Conferva aerea* Dillwyn. 1806. Syn. of Brit. Conf.

TYPE: *Conferva aerea* Dillwyn. 1806. Syn. of Brit. Conf. Tab. 61.

Type Locality: Yarmouth Beach, England.

Chaetomorpha princeps Küt. 1849. Sps. Alg. P. 380.

Conferva princeps Küt. 1843. Phyco Gen. p. 206.

Chaetomorpha variabilis Küt. 1849. Sps. Alg. p. 378; 1853. Tab. Phyc. III t. 55.

Conferva variabilis Küt. 1843. Phyco. Gen. P. 260.

Chaetomorpha dubyana Küt. 1849. Sps. Alg. p. 378; 1853. Tab. Phyc. III t. 57 f. 3.

Conferva dubyana Küt. 1843. Phyco. Gen. p. 260.

Chaetomorpha linum (Müller) Küt. f. *aerea* Dillw. sensu Collins 1918. Grn. Alg. of N. Amer. Sup. p. 79; Farlow, 1881. Mar. Alg. of New Eng. and Adj. Coast. p. 46

Chaetomorpha aerea (Dillwyn) Küt. f. *aerea* (Dillw.) Collins. 1909. Grn. Alg. of N. Amer. p. 324.

Chaetomorpha linum (Müll.) Küt. sensu Abbot and Hollenberg. 1976. p. 101 (in part).

The species (Fig. 5) grows attached by a discoid basal cell and is often found growing in turf-like masses. Cell diameters range from 125–400 μm (600 μm when fertile), except for the basal cell, which is somewhat narrower and attenuated basipetally. The LWR of the upper cells is 1.5 to 2.5, while the basal cells range between 3 and 8 (Fig. 6).

Distribution and Ecology

The species has a world-wide distribution, from the Pacific and Atlantic coasts of the U.S.A., and from Canada, Norway, France, Spain, South Africa, Australia, the Philippines, Japan, and China. In New England, it grows in open coastal littoral pools within the mid and upper littoral zone. No estuarine records are known. *Chaetomorpha aerea* is found all year. It has an isomorphic alternation of generations (Hartman, 1929) and is reported to form zoospores in early summer (Taylor, 1957).

Figures 5 and 6. *Chaetomorpha aerea*. Fig. **5,** habit of *C. aerea*. Fig. **6,** basal region of filament with holdfast cells (Scale = 200 μm).

Representative specimens:

Australia. Rottrest Is., *Nash & Nash 41* (UC). Kangaroo Is., *Womersley s.n.*, April 1949 (UC). **Austria.** Flora Exsicc. Austro-Hungarian 1590 (FH). **Canada.** NEWFOUNDLAND: Bonne Bay, *Hooper & Roberge 8939* (NFLD). **Canary Islands.** Las Palmas, *Børgesen 4058* (UC). **Chile.** Chiloe, *Hieneck & Meerlagen 254* (UC). **China.** Fukien, *Chood A891* (UC); *Tsingyao 83* (UC). **Cuba.** Bahia Matanzos, *Dawson 7755* (UC). **France.** Bonflavor, *Thurst 156* (FH). Cherbourg, *Thurst 157* (FH). **Great Britain.** *Collins 86* (FH). **Italy.** Cagliori, Canepa Erb. Criff Stal. Ser. II 778–779 (UC). Genova, Canepa Erb. Criff Stal. Ser. II 361 (UC). **Jamaica.** Port Antonis, *Pease & Buttler s.n.*, July 1894 (FH). **Japan.** Tsugaru Strait, *Rosenbaum s.n.*, 30 July 1917 (UC). **Jugoslavia.** Trieste, Alg. Adriatacae Exsicc. 36 1911 (FH); *Hoeneck & Meerlagen 305* (UC). **Mexico.** Bihiak, *Dawson 1079* (UC). Punta Rosalia, *Dawson 2830* (UC). **New Zealand.** Bay of Islands, *Nash & Nash 347* (NFLD). **Norway.** Lille Svartskjar, Folsie, Witt. & Nord. Alg. Exsicc. 946 (UC). **Puerto Rico,** *Patillor, Alamodovar & Rolad 4218* (UC). **South Africa.** East Landon, *Niekirk 42* (UC). **Spain.** Borquera, *Sauvageau s.n.*, September 1896 (FH). **Sweden.** Bohuslan, *Kylin s.n.*, 8 July 1907 (UC).

United States. CALIFORNIA: Orange Co., Laguna Beach, *Mathieson s.n.*, 23 June 1969 (NHA); Monterey Co., Monterey Pen., *Mathieson s.n.*, 26 June 1960 (NHA), *Doty 4336* (FH). Pt. Fermin, Gardner Algae dist. from U. of California 37 (UC). San Diego Co., San Diego, *Collins, Holden & Setchell 76* (NHA); La Jolla, *Dawson 9566* (UC). MAINE: Hancock Co., Gouldsboro Bay, *Taylor s.n.*, 18 August 1960 (FH); Reid State Park, *Whittick & Hooper 6754* (FH). MASSACHUSETTS: Essex Co., Magnolia, *Clark s.n.*, 25 October 1889 (FH). NEW HAMPSHIRE: Rockingham Co., Seabrook, *Wells s.n.*, 21 September 1966 (NHA). Dover, *Mathieson s.n.*, 3 October 1977 (NHA). Newcastle, *Mathieson s.n.*, 20 June 1966 (NHA). Portsmouth, *Lamb A-99* (FH).

Taxonomic History

Chaetomorpha aerea (Dillwyn) Kützing was initially described as *Conferva aerea* (Dillwyn, 1806). The species was described as basally attached in tufts and being as "brittle as *C. capillaris*" (= *C. linum*) "but not at all curled or entangled as that species."

The possible conspecific relationship between *Chaetomorpha linum* and *C. aerea* was first expressed by Rosenvinge (1893), by stating the belief that *C. linum* was a detached state of *C. aerea.* Subsequently, the two have been designated as forms of one species by some authors and as distinct species by others. For example, Collins (1909) formally designated *C. linum* as a form of *C. aerea (C. aerea* f. *linum).* He later (Collins, 1918) stated that *C. linum* had priority over *C. aerea* and classified the taxa *C. linum* f. *linum and C. linum* f. *aerea,* respectively. Christensen (1957) showed apparent transitional stages between attached *(C. aerea)* and detached *(C. linum)* entities and followed Collins' (1918) nomenclature. Price (1967) also favored a forma designation for the two taxa, and

expressed the opinion that no conclusive evidence had been shown for recognition at the specific rank. In contrast, Taylor recognized two distinct taxa *(C. aerea* and *C. linum)* but stated no justification. Patel's (1971a) cytological studies support Taylor's classification, reporting $n = 18$ in *C. linum* and $n = 12$ in *C. aerea*. Further evidence for their separation was given by Kornmann (1972), who showed that the taxa exhibited independent isomorphic alternation of generations. That is, *C. linum* showed a complete life history while *C. aerea* recycled itself by means of bi- or quadraflagellate zoospores. Most recently, biochemical information concerning genetic differences has been outlined by Blair et. al. (1982). Thus, evidence is present for the retention of two distinct taxa.

Chaetomorpha melagonium (Weber et Mohr) Kützing 1845. Phyco. Germ. P. 204

Basionym: *Conferva melagonium* Weber et Mohr. 1804. Naturhistorische Reise durch einen Teil Schwedens. p. 149 t. 3, f. 2a & 2b.

TYPE: unknown

Type locality: North Sea

The species (Fig. 7) is common in low littoral pools and within the sublittoral zone to 15 m below MLW. The plants usually occur in clumps but single filaments are not infrequent, particularly in estuarine locations. The cells are 350–750 μm (less than 1000 μm) diameter. The filaments are attached by a single discoid basal cell, which is attenuated and 8–14 times longer than broad. The LWRs of the cells just above the holdfast cell are 4–8 (Fig. 8), decreasing to 1.0–2.0 in the upper portions of the filament (Fig. 9). The species is believed to have an isomorphic alternation of generations, although gametic fusion has not been verified (Kornmann, 1972; Patel, 1972).

Distribution and Ecology

Chaetomorpha melagonium is a northern species ranging from Long Island Sound to Labrador on the Atlantic coast of North America, and from Oregon to Alaska on the west coast. It occurs primarily in open coastal habitats but scattered estuarine records are known from areas with salinities greater than 20 ppt. The species is found throughout the year. Patel (1972) records zoospore produc-

Figures 7–9. *Chaetomorpha melagonium*. Fig. **7,** habit of *C. melagonium*. Fig. **8,** basal region of filament with holdfast cell. Fig. **9,** upper portion of filament showing the decrease in cell LWR (Scale Fig. 8 and 9 = 50 μm).

tion in February. He also observed gamete production but no fusion. Kornmann (1972) recorded bi- and quadriflagellated zoospores in culture but he did not summarize a reproductive phenology.

Representative specimens:

Canada. NEWFOUNDLAND: Biscay Bay, *Hill 5247* (NFLD), *Hooper 6105* (NFLD). Placentia Bay, *Hooper, Roberge & Reddin 12279* (NFLD). LABRADOR; N. Green Island, *Hooper 8557* (NFLD). NOVA SCOTIA; Tenenee Cove, *Hooper & Wittick 13700* (NFLD). QUEBEC: Cacouma Co., *Cardinal s.n.*, 22 June 1971 (NFLD).

United States. ALASKA: Commander Islands, *Stejnegia 1889* (FH). Juneau, *Saunders 243* (FH). MAINE: Hancock Co., Gouldsboro Bay, *Taylor s.n.*, 18 August 1960 (FH). Mt. Desert, *Holden s.n.*, 12 August 1889 (FH). MASSACHUSETTS: Essex Co., Magnolia, *Clarke s.n.*, 25 October 1889 (FH). Nanhunt, *Young 1884* (FH). NEW HAMPSHIRE: Rockingham Co., Fort Stark, *Mathieson s.n.*, 20 June 1966 (NHA). Dover, *Mathieson s.n.*, 3 October 1977 (NHA). Isle of Shoals, *Lamb A-99* (FH). Rye Ledge, *Newhouse s.n.*, 20 October 1951 (NHA).

Taxonomic History

Conferva melagonium was described by Weber and Mohr (1804) and transferred to the genus *Chaetomorpha* by Kützing (1849). There has been relatively little confusion regarding this species since that time. *Chaetomorpha picquotiana* had been regarded as a form of this species but has been shown to be a separate entity (see taxonomic history of *Chaetomorpha picquotiana*, p. 183)

Chaetomorpha brachygona Harvey. 1857 Ner. Bor.-Amer. P. 88

TYPE: *Chaetomorpha brachygona* Harvey. 1857. Ner. Bor. Amer. p. 88, t. 46.

Type locality: Key West, Florida

Chaetomorpha tortuosa Maze and Schramm. 1870–77. de Classif. des. alg. dela Guadeloupe. XIX

Rhizoclonium capillarae Vickers. 1905. List des Alg. Mar. del la Barbade. Ann. Sci. Nat. Bot. **IX:** 45 66.

The morphology and habit of this species are similar to that of *Chaetomorpha linum*, with the exception of its narrower dimensions. The entangled filaments of *C. brachygona* have cell diameters of 80–150 μm and LWRs of 1 to 3 (less than 4; Fig. 10). The plant reproduces by vegetative reproduction (i.e., fragmentation) and an isomorphic alternation of generations is assumed.

Distribution and Ecology

Figure 10. *Chaetomorpha brachygona* (Scale = 50 μm).

The plant seems to have the same latitudinal distribution as *Chaetomorpha linum*. Previously *C. brachygona* was recorded only from North Carolina and the tropics. Its previous confusion with *C. cannabina* and *C. capillaris* has probably restricted its delineation in northern latitudes (see taxonomic history). The species occurs in coastal as well as a variety of estuarine habitats if adequate substratum is available.

Representative specimens:

Bermuda. Hamilton Island, *Harvey s.n.* (FH). St. George's Island, *Lamb & Fralick A-401* (FH). **Canada.** BRITISH COLUMBIA: *Trocl & Grant s.n.*, 17 April 1975 (NFLD). NEWFOUNDLAND: Bonavista Bay, *Kells, Hill 4194* (NFLD); *4273* (NFLD). **France.** Albères, *Straus s.n.*, August (NHA). Cannes, Wit., Nord., Lager Algae Exsicc. 1435 (UC). **Great Britain.** British Isles, *Dixon 11* (FH). **India.** Orientalis, *Børgesen 5310* (UC). **Italy.** Naples, *Reed s.n.*, 9 March 1911 (UC). **Jamaica.** *Manchoinial s.n.* (FH). **Japan.** Okanuma, Algae Japanicae Exsicc. 93 (FH). **Jugoslavia.** Trieste: Adriaticae Exsicc. 37 (FH). **New Zealand.** Bay of Islands, *Nash & Nash 3469* (NFLD). **Philippines.** Montalben, *Merril 5096* (FH). **Samoa.** Tutulia Islands, *Setchell 1029* (UC). **Tahiti.** South Peninsula, *Bartlett 17962* (FH). Society Islands, *Setchell & Parks 5182* (UC).

United States. ALASKA: New Merlakahtla, *Saunders 46* (UC), *417* (UC). HAWAII: Molakai, *Reed 314* (UC). MAINE: York Co., Kittery, *Mathieson s.n.*, 12 October 1977 (NHA). Bar Harbor, *Leary s.n.*, 15 May 1971 (NHA). NEW HAMPSHIRE: Rockingham Co., Newington, *Mathieson s.n.*, 18 July 1975 (NHA). Newcastle, *Mathieson s.n.*, 23 July 1966 (NHA). WASHINGTON: San Juan Island, *Zeller 1298* (UC). **Australia.** North Queensland: *May NSW 126964* (NFLD).

Taxonomic History

The species was first described by Harvey (1857). No dimensional characteristics were given other than that the cells were "as much as, or much shorter than their diameter", and that this species was a more "robust" plant than *Rhizoclonium tortuosum*. The accompanying illustration (Harvey, 1957; Pl. XLVI-A) had no scale, and in comparison, was not noticeably larger than the diameter illustrated for *Rhizoclonium tortuosum* (Harvey, 1857; Pl. XLVI-B). The dimensional characteristics later applied to this species varied somewhat but were in general agreement. The recorded distribution of this species appears to have been restricted due its misidentification as *Chaetomorpha capillare* (Küt.) Børg. (= *Rhizoclonium tortuosum* (Dillw.) Küt.), and *Chaetomorpha cannabina* (Aresch.) Kjellm. (Table 1) owing to variations in measurement attributed to these last 2 species. The variation is partially a reflection of misidentification distributed in exisccatae. For example, specimen #1435 in Alg. Ag. Dulc. Exisc. as *Rhizoclonium capillare* and #135

Table 1. **Dimensions of *Chaetomorpha cannabina* given in literature**

AUTHOR	WIDTH	LENGTH
Areschoug 1843	1/32‴–1/25‴ (66μm–84μm)	2–4 times longer than broad
Areschoug 1850	0.1–0.2mm	3–4 times longer than broad
Kützing 1849 (as *Cladophora cannabina*)	1/35‴–1/15‴ (60–40μm)	3–5 times longer than broad
Collins 1909	75–100μm	3–8 times longer than broad (500–600μm)
Setchell & Gardner 1920	45–150μm	3–8 times longer than broad (500–600μm)
Scagel 1966	75–100μm	3–8 times longer than broad (200–450μm)
Taylor 1957	75–100μm	3–8 times longer than broad (500–600μm)
Edelstein & McLachlan 1967	50–60μm	7 diameters

in Alg. Scand. Exisc. fasc. II as *Chaetomorpha cannabina* should properly be identified as *Chaetomorpha brachygona*. For further discussion of the taxonomy of *Chaetomorpha capillare* (Kütz.) Børg. see the taxonomic history of *Rhizoclonium tortuosum* (p. 201).

Chaetomorpha minima Collins and Hervey. 1917. The Algae of Bermuda. Pro. Amer. Acad. Arts and Sci. Vol. 53.

TYPE: *Chaetomorpha minima* Collins and Hervey. Herb. Collins.

Filaments attached by a basal cell, erect to approximately 10 mm (Fig. 11), cells cylindrical, 24 to 40 μm diameter, 2 to 4 times as long as broad, and occasionally constricted at the end walls.

Figure 11. *Chaetomorpha minima* (Scale = 50 μm).

Distribution and Ecology

The plant was found as an epiphyte on *Chaetomorpha aerea and C. melagonium* during the summer and fall of 1977. Previously it was recorded only from the tropics (Taylor, 1960). The New England records of *C. minima* dramatically extend the known distributional limits of the species. Further investigations should demonstrate whether it has a continuous or scattered (disjunct) distribution.

Representative specimens:

United States. MAINE: York Co., Kittery, *Mathieson s.n.*, 12 October 1977 (NHA); *Hehre s.n.*, 19 November 1976 (NHA).

Taxonomic History

The species was described from tropical water, as a fine (10 20 μm), short (<5mm) filament. The author has some reservations regarding the proper designation of this plant. The dimensions of the New England filaments represent an extension beyond the measurements of the type material. The only other species with which the New England material could compare is the Pacific *Chaetomorpha californica* Collins. However, differences lead to exclusion of this species as being equivalent to the New England material. *Chaetomorpha californica* is stated as having a basal cell to 200 μm (noticably elongate) and constricted at the base. Further, the filaments may attain a length of 20 cm. The basal cell of the New England material is neither noticably elongate nor constricted at the base. The greatest length of a filament seen in the New England material was 10 mm. Considering the well documented cell size variability of the unbranched species of Cladophoraceae it is considered that the placement of *C. minima* on the New England material is correct.

It should be noted that *C. minima* falls within the dimensional range of *Rhizoclonium riparium* and just outside that of *R. tortuosum*. Reports of Perrot (1965) and Neinhuis (1975) concerning the attached phases of the above species suggest the possibility of *Chaetomorpha minima* representing an attached form of a *Rhizoclonium* species. However, further investigation of the species will be needed to clarify any possible relationships.

RHIZOCLONIUM

Rhizoclonium Kützing. 1843. Phyco. Gen. p. 261.
Lectotype: *Rhizoclonium jurgensii* (Mert.) Kütz. Jurgens Alg. ag. 1816–22. Decas II #6 (L). (Koster, 1955)
Type locality: North Sea.

The genus *Rhizoclonium* contains species of unbranched, uniseriate filaments. The cells are uni- to multinucleate with a single parietal reticulate chloroplast, which often fragments with age. Few to many pyrenoids are present depending upon the age and size of

the cells. The filaments can occasionally be attached by a basal cell. The LWRs of the cells are 1 to 4 (less than 6). The filaments adhere to coarse algae and other substrates by rhizoidal projections. Filaments tend to show a greater number of proliferations on soft substrata than on hard substrata (Nienhuis, 1975). Reproduction is by fragmentation and by an isomorphic alternation of generations with iso- or anisogamous biflagellate gametes and quadriflagellate zoospores as well possible recycling of their sporophytic stage with bi- or quadriflagellate zoospores (Patel, 1971a).

KEY TO THE NEW ENGLAND SPECIES OF *RHIZOCLONIUM*

1. Filaments entangled with few to many rhizoidal proliferations, 8 to 48 μm diam., from marsh areas and high littoral pools, reproduction by isogamous gametes ... *R. riparium* p. 203.
1. Filaments entangled in coarse algae in the mid-low littoral zone and sublittoral zones, few or no single celled rhizoidal proliferations; cells 30 to 75 μm diam., reproduction by anisogamous gametes. ..... *R. tortuosum* p. 198.

Rhizoclonium tortuosum (Dillwyn) Kützing. 1845. Phyco. Germ. p. 203

Basionym: *Conferva tortuosa* Dillwyn. 1806. Brit. Conf. Fasc.

Type: Not in existence (Chapman, 1939)

Type locality: Swansea, England

Chaetomorpha capillaris (Kützing) Børgesen. 1925. Mar. alg. of Canary Is. p. 45.

Chaetomorpha tortuosa Kützing. 1849. Sps. Alg. p. 376.

Rhizoclonium capillarae Kützing. 1847. Bot. Zietg. p. 166.

Conferva tortuosa C. Agardh. 1824. Sys. Alg. p. 98.

Conferva tortuosa J. Agardh. 1842. Alg. Mar. Med. et Adri. p. 12.

Rhizoclonium riparium (Roth) Harvey f. *validum* Folsie 1878-88. Witt. & Nord. Alg. ag. Duc. exiscc. #624.

Lola implexa (Harvey) Perrot 1965. C.R. Acad. Sci. Paris Group 11. **261:** 503 506.

Chaetomorpha tortuosa (Dillw.) Kleen. 1847. Om Nordlanders Hogra Hafsalger. p. 45.

The species is a common inhabitant of the low littoral and upper sublittoral zones where it grows in clumps in tide pools, entangled among coarse algae or as "wooly" skeins across bare rocks. The filaments are tortuous and densely entangled, with cell diameters of

24 to 75 μm. The LWRs of the cells are usually 2 to 3 but they may be 1 to 4 (Fig. 12). Rhizoidal proliferations are rare in New England material, and if found they are single-celled. The species has an isomorphic alternation of generations with anisogamous gametes (Fig. 13) and quadriflagellate zoospores (Hamel, 1929).

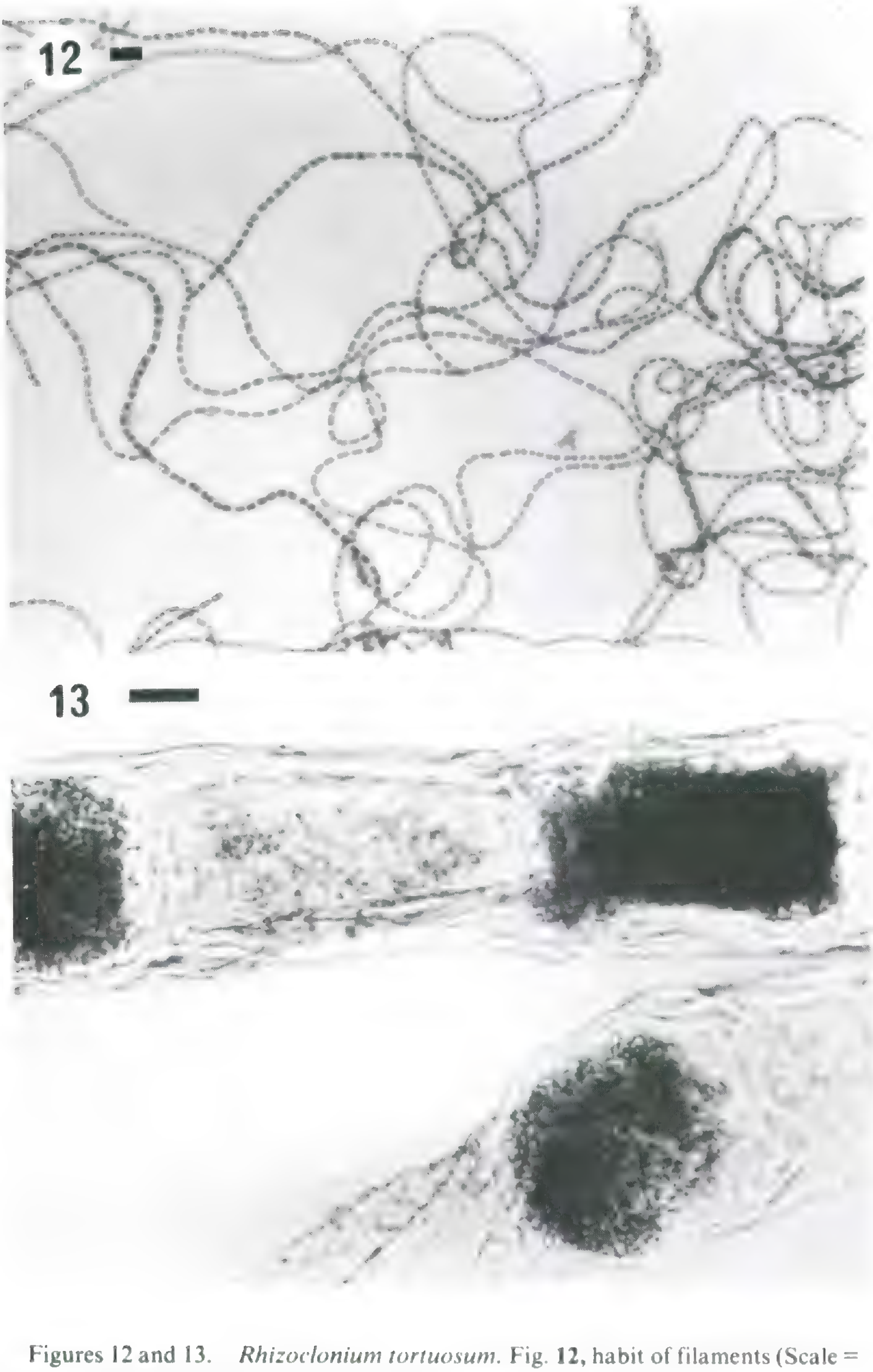
Distribution and Ecology

Rhizoclonium tortuosum shows a broad geographical distribution extending from Florida to Labrador, and Southern California to Alaska on the coasts of the United States, and from France, Norway, the Philippines, and Formosa. In New England, it is most common in the littoral region on the open coast but it survives in estuarine habitats where the salinities approximate 15 ppt.

Representative specimens:

Azores. San Miguel, *Canneiro 755* (UC). **Bermuda.** Paget Island, *Bernatowicz 51–764* (UC). **Canada.** BRITISH COLUMBIA: Felix Bay, *Root & Grant s.n.*, 17 April 1975 (NFLD). NEWFOUNDLAND: Allan's Lighthouse, *Hooper 7401* (NFLD). Bonne Bay, *Hooper & Gibbons 11197* (NFLD); Conception Bay, *Hill 3321* (NFLD); Gros Morne Park, *Hooper, Gibbons & Roberge 11710* (NFLD). NOVA SCOTIA: Annapolis Co., Tammy's Beach, *Parsons 6* (NFLD). QUEBEC: *Cardinal s.n.*, 11 August 1971 (NFLD). **Canary Islands.** Las Almas, *Børgesen 3916* (UC). **France.** Algeres, Hauk et Richter Phyco. Univer. 728 (UC). **Formosa.** Diabouratsu, *Yamada 272789* (UC). **Netherlands East Indies.** Pali, *Yong Sehg B282* (UC). **Norway.** Novegia, Christionsand, Ekman in Alg. Scand. Exsicc. Ser. Fasc. Primus 29 (UC). **Philippines.** Luzon, *Merrill 7456* (UC); Camiguin Island, *Setchell & Parks 5160* (UC).

United States. ALASKA: Tutkutat Bay, *Saunders 192* (UC); Kodiak, *Setchell & Lawson 5141* (UC); Orca, *Setchell & Lawson 5269* (UC). CALIFORNIA: Los Angeles Co., Long Beach, *McClatchie 1171* (UC); Point Lobos, *Gardner 3396* (UC); Monterey Co., Carmel River, *Doty 5868* (UC); San Mateo Co., Moss Beach, *Doty 6055* (UC). FLORIDA: Monroe Co., Key West, *Hitchcock s.n.*, (NHA). HAWAII: Keaukaha, *Setchell & Setchell 10133* (UC). MAINE: Cumberland Co., Reid State Park, *Britt s.n.*, 15 July 1967 (NHA); Washington Co., W. Quoddy Head, *Searles 215D* (NHA); York Co., Eliot, *Searles s.n.*, 2 July 1966 (NHA); Kittery, *Blair s.n.*, 20 December 1977 (NHA); Isle of Shoals, *Blair s.n.*, 16 April 1976 (NHA). MASSACHUSETTS: Barnstable Co., Woods Hole, *Newhouse s.n.*, 14 July 1951 (NHA); Essex Co., Salem, *Femino s.n.*, 22 July 1966 (NHA); Cape Ann, *Searles s.n.*, 2 May 1966 (NHA). Nanhaunt, Collins Phyco. Univ. 627E (UC). NEW HAMPSHIRE: Rockingham Co., Isles of Shoals, *Conway & Shipman s.n.*, 22 July 1966 (NHA); Newcastle, *Tveter s.n.*, 20 October 1973 (NHA); Rye, *Hehre & Conway s.n.*, 8 January 1966 (NHA); Strafford Co., Durham, *Mathieson s.n.*, 11 August 1977 (NHA). Dover, *Conway & Shipman s.n.*, 16 August 1966 (NHA). NEW YORK: Putnam Co., Cold Spring Harbor, *Broon s.n.*, 23 July 1908 (UC). OREGON: Coos Co., Sunset Bay, *Phinney & Hanson 282* (UC); North Bay, *Hanson s.n.*, 289 (UC). RHODE ISLAND: Newport Co., Cloud Point, *Setchell s.n.*, 17 June 1923 (UC). WASHINGTON: Clalham Co., Friday Harbor, *Gardner 4083* (UC); San Juan Is., *Setchell & Gardner 219* (UC).



Figures 12 and 13. *Rhizoclonium tortuosum*. Fig. **12,** habit of filaments (Scale = 150 μm). Fig. **13,** reproductive cell with anisogametes (Scale = 10 μm).

Taxonomic History

The species was originally described by Dillwyn (1806) as *Conferva tortuosa*. No dimensional characters are given in the description, other than the statement that "the filaments are fine as hair of the human head", and that the cells are nearly twice as long as broad. A type specimen was not designated and the published drawing shows no scale. Chapman (1939) was unable to find a type specimen but succeeded in finding a specimen identified by Dillwyn as *Conferva tortuosa*. The filaments were 34 to 48 μm diam. with a mean of 40 μm, and were 1 to 2 times as long as broad. Kützing (1845) transferred *Conferva tortuosa* Dillwyn to *Rhizoclonium tortuosum*, stating that its diameter was 1/70‴ (‴ = a ligne or 2116 μm) or 31 μm wide and 1 to 1.5 times as long as broad.

Confusion arose between *Rhizoclonium tortuosum* and Kützing's (1849) *Chaetomorpha tortuosa*. The confusion was examined by Chapman (1939) and will only be reviewed here. To examine this confusion we must look back to the origins of *C. tortuosa* and *Rhizoclonium capillare* (Kützing, 1847). The species *R. capillare* was characterized by cells measuring 1 45‴ (47 μm) and 1 to 2 times longer than broad. Later Kützing (1849) described *Chaetomorpha tortuosa* stating it was characterized by cells 1/45‴ to 1/40‴ (47 to 57 μm) in diameter, rigid, curled, tortuous, and 1 to 2 times as long as broad. *Rhizoclonium capillare* Kützing was placed as a synonym of *Chaetomorpha tortuosa*. The basionym cited by Kützing for both *Chaetomorpha tortuosa* and *Rhizoclonium capillare* is *Conferva tortuosa* J. Agardh, which is based on *Conferva tortuosa* C. Agardh (J. Agardh, 1842). *Conferva tortuosa* C. Agardh is in turn based on *Conferva tortuosa* Dillwyn (C. Agardh, 1824). However, *Conferva tortuosa* Dillwyn is the basionym for *Rhizoclonium tortuosum* (Dillwyn) Kützing (1845). Thus, there had been an inadvertent establishment of two species on a single basionym. Therefore, either the two species are united under one name (brought into synonymy), or if two species are separate entities, the invalid name is discarded and the second species is renamed. An examination of the original description for *R. capillare* and *R. tortuosum* indicates that Kützing's original intent was to describe two separate taxa. The cells of *Rhizoclonium tortuosum* were listed as 1/70‴ (31 μm) diameter and 1.5 times longer than broad (Kützing, 1845), while *R. capillare* cells were described as being 1/45‴ (47 μm) diameter and 1 to 2 times

longer than broad (Kützing, 1847). Børgesen (1925) noted Kützing's intent to describe two separate species, and the incorrect basionym declaration. Accordingly, he made the combination *Chaetomorpha capillare* (Kützing) Børgesen citing *R. capillare* as the basionym. The continued confusion as to the proper naming and dimensional characteristics of *C. capillare* is evident in a variety of recent studies (Kornmann & Sahling, 1977; Christensen, 1975; Price, 1967) which cite the taxon as either *C. tortuosa* or *C. capillare*. However, recent work (Blair, 1978) has shown *Chaetomorpha capillare* (Kützing) Børgesen and *Rhizoclonium tortuosum* to be conspecific on the basis of morphological continuity and indistinguishable habit. Thus, *C. capillare* (Kütz.) Børg. and *R. capillare* Kütz. are synonyms of *R. tortuosum* (Dillw.) Kütz.

Foslie (in Wittrock & Norstedt, 1877-1887) described *Rhizoclonium riparium* (Roth) Harvey f. *validum* Foslie stating that the form was wider and had a greater length than *R. riparium*, being 26 to 36 μm wide, 0.25 to 2.33 times longer than broad, and without rhizoids (Koster, 1955). Rosenvinge (1893) elevated the form to varietal status, increased the width range to 30 50 μm, and indicated that rhizoids could be numerous. Some authors (Stockmayer, 1898; Chapman, 1939) have reduced *R. tortuosum* to synonymy under *R. riparium* f. *validum*, while Koster (1955) preferred to synonymize *R. riparium* f. *validum* under *R. tortuosum*, which would be the correct synonymy on the basis of priority of publication. Therefore, *R. riparium* f. *validum* was also placed as a synonym of *R. tortuosum* (Koster, 1955).

Hamel (1929) showed that *Rhizoclonium lubricum* Setchell et Gardner exhibited anisogamous reproduction. The character is unique within the Cladophoraceae and led to the establishment of *Lola* Hamel for unbranched cladophoralean algae with anisogamous reproduction. Perrot (1965) later showed that *Rhizoclonium implexum* Harvey (= *R. tortuosum* (Dillwyn) Kützing; see Chapman, 1939) has anisogamous reproduction. Accordingly he transferred *R. implexum* to *Lola*. Presently the species is referred to as either *Rhizoclonium tortuosum* (Dillwyn) Kützing or *Lola tortuosa* (Dillwyn) Perrot. It should be noted that the establishment of a genus on a single characteristic (i.e., anisogamous reproduction) despite other similarities with the *Rhizoclonium* sp. is tenuous. The use of anisogamous reproduction as a generic character is further

questionable in light of the fact that other green algal genera, (i.e., *Sphaeroplea, Chlamydomonas*) contain species that range from isogamous to anisogamous. The present author, therefore, favors the retention of *Rhizoclonium tortuosum* in the genus *Rhizoclonium*.

Rhizoclonium riparium (Roth) Harvey. 1846. Phyco. Brit. IV p. 1238

Basionym: *Conferva riparia* Roth. 1797. Catal. Bot. Fasc. 1.

Type: *Conferva riparia* Roth leg. Mertens. 1803. Norderney, Germany ex Herv. Hooker (K).

Type Locality: Morderney, Germany.

Rhizoclonium jurgensii (Mertens) Kützing. 1843. Phyco. Gen. p. 261.
R. lacustre Kützing 1847. Diag. Verner. odea Dritis. Alg. Bot Ziet.
R. implexum (Dillwyn) Kützing. 1845. Phyco. Germ. p. 206.
Conferva implexa Dillwyn. 1806. Brit. Conf. p. 46 t. b.
Rhizoclonium interruptum Kützing. 1849. Sps. Alg. p. 384; 1853. Tab. Phyc. III t. 69, f. 2.
R. kerneri Stockmayer. 1898. Uber die Algen. p. 583.
R. kochianum Kützing. 1845. Phyco. Germ. p. 206.

The species is found in high tide pools and marshes on the open coast as well as within high marsh communities in estuaries. The filaments are lax and entangled, with a cell diameter of 8 to 45 μm diameter. The LWRs vary between 1 and 4 (< 6). Rhizoidal proliferations are sparse to abundant in New England material, and consist of single or multiple cells. The plant has never been found attached (basally) in New England although it shows an attached stage in culture (Neinhuis, 1975). *Rhizoclonium riparium* exhibits an isomorphic alternation of generations with isogamous gametes and bi- and quadriflagellate zoospores (Neinhuis, 1975).

Distribution and Ecology

Neinhuis (1975) and Koster (1955) have given extensive summaries of the ecology and distribution of the species. Accordingly only an overview is given and reference is made to the above articles for a variety of details on the plant's distribution and ecology. *Rhizoclonium riparium* has a world-wide distribution, being recorded from the Netherlands, Europe and Japan. It is extremely euryhaline, being found in a broad range of estuarine and coastal habitats. Within the Great Bay estuary system *R. riparium* is usually found entangled among the bases of *Spartina alterniflora* on muddy sub-

strata within the littoral zone, also reaching the headwaters of many riverine tributaries. Some samples of *R. riparium* may reach the dimensions of *R. tortuosum*, from which it may be separated by its broader estuarine distribution and differential reproductive morphology, i.e., isogamous for *R. riparium* and anisogamous for *R. tortuosum*.

Representative specimens:

Canada. NEW BRUNSWICK: Charlottes Co., Campobello Island, *Hehre & Conway CI911* (NHA); South Wolf, *Conway et al. W-77* (NHA). NEWFOUNDLAND: Bonne Bay, *Hooper & Williams 7977* (NFLD), Bonavista Bay, *Mathieson NF202* (NHA); Conception Bay, *South et al. 4509* (NHA). **Tahiti.** Society Islands, *Setchell & Parks s.n.*, July 1922 (UC), *Hoenneck & Meerlagen 478* (UC).

United States. DELAWARE: Lewes, *Mathieson et al. s.n.*, 14 August 1966 (NHA). MAINE: Aroostook Co., Eagle Island, *Collins 2116* (NHA); Hancock Co., Camden, *Hooper 951* (NHA); Washington Co., Lubec, *Hehre 3182* (NHA); York Co., Ogunquit, *Searles s.n.*, 7 April 1966 (NHA); Eliot, *Searles s.n.*, 30 April 1966 (NHA). NEW HAMPSHIRE: Rockingham Co., Greenland, *Mathieson & Hehre s.n.*, 14 September 1966 (NHA), *Hehre et al. s.n.*, 8 July 1966 (NHA); Newington, *Mathieson s.n.*, 9 September 1977 (NHA); Hampton, *Mathieson s.n.*, 11 September 1969 (NHA); Portsmouth, *Croasdale s.n.*, 28 July 1938 (NHA), *Blair s.n.*, 17 August 1977 (NHA); Newcastle, *Mathieson s.n.*, 20 April 1967 (NHA); Strafford Co., Durham, *Mathieson s.n.*, 20 June 1966 (NHA); Dover, *Hehre & Shipman s.n.*, 24 June 1966 (NHA); Durham, *Mathieson s.n.*, 27 July 1977 (NHA); Newington, *Reynolds NB381* (NHA).

Taxonomic History

This species was first described by Roth (1793) as *Conferva riparia* based upon its thin, twisted, bifurcating habit (*"apice tantum divisa et pierumque bifia"*). No dimensional characters were given, other than that the width was one half the length, (*"diametro sesquilongioribus"*). In addition, no type specimen nor drawing was indicated. Koster (1955) found a specimen of *Rhizoclonium riparium* collected by Mertens from the type locality of Norderney, Germany. She assumed that it was part of the type collection. The specimen contained a mixture of *Rhizoclonium riparium* (Roth) Harvey and *Caldophora fracta* (Dillwyn) Kützing f. *haukii* (Børgesen) Slootweg. Koster felt the *Cladophora* fraction of this specimen pertained to Roth's description of branching. Harvey (1845-51), when transferring the species from *Conferva* to *Rhizoclonium*, selected only the *R. riparium* element from the mixture (Koster, 1955). Accordingly, Koster proposed that the specimen from Norderney, Germany, in the Kew Herbarium should be designated as a lectotype.

The filaments are 18 to 30 μm wide and cells are 1.5 to 2.5 times longer than broad (Koster, 1955).

Specimens that have been identified as *Rhizoclonium riparium* are commonly found, but the degree of rhizoidal proliferation is variable. As a result a large number of forms and varieties have been described depending upon the presence, absence and morphology of rhizoids. For example, *R. riparium* (Roth) Harvey var. *polyrhizum* (Lyngbye) Rosenvinge is described as having many rhizoids with one to few cells, while *R. riparium* (Roth) Harvey var. *implexum* (Dillwyn) Rosenvinge is recorded to have few or no rhizoids. Koster (1955) proposed the distinction of *"status radicans"* and *"status arrhizum"* for those specimens with a variable occurrence of rhizoids with the belief that rhizoidal proliferations were influenced by environmental factors.

Nienhuis (1975) recorded extreme variability of filament and rhizoidal morphology for *Rhizoclonium riparium* populations in the Netherlands. After extensive field and culture studies, he found that filament diameter and the degree and size of rhizoidal proliferations were influenced by tidal elevations, firmness of substrates, and salinity. The rhizoidal variability he observed encompassed the morphologies recorded for *R. implexum* (Dillwyn) Kützing (Kützing, 1849), *R. hieroglyphicum* (C. Agardh) Kützing (Kützing, 1849) and *R. riparium* (Roth) Harvey. As a result he synonymized *R. implexum* and *R. hieroglyphicum* with *R. riparium* (Roth) Harvey.

DISCUSSION

As reflected in the Taxonomic History sections of this paper, a great deal of confusion concerning specific delineation has existed within these genera. While the present report addresses some of the questions that have arisen, many more remain unanswered. For example, difficulties may arise in discerning non-reproductive *Rhizoclonium tortuosum* and *R. riparium* within the region of dimensional overlap (24 to 45 μm). Habitat information may aid in their determination as *R. tortuosum* is found in the low littoral to upper sublittoral while *R. riparium* is found in areas of extreme environmental fluxes, such as marshes and mudflats. The differential reproductive phenology, however, confirms the need for specific separation of the two species (*Rhizoclonium tortuosum* showing

anisogamous reproduction while *R. riparium* reproduces isogamously).

Within the genus *Chaetomorpha*, questions arose as to the taxonomic validity of *Chaetomorpha cannabina* (Aresch.) Kjell. as no specimens examined (field or herbarium) fit the dimensions cited for the species. In general, the species is considered to vary in diameter from 75 to 100 μm with cell lengths being 3 to 8 diameters (500 to 600 μm) long (Taylor, 1957). The dimensions credited to this species have varied considerably from author to author (Table 1). Areschoug (1843) described the species *Conferva cannabina*, and distributed specimens of the species in the Algae Scandinavicea Exsiccatae (1840). Areschoug (1843) referenced a previously published species, *Conferva auricoma* Suhr (Suhr, 1840) stating that through communication with Suhr, it was believed that the two plants were the same. If in fact the two species are the same then the correct designation of the taxon should be *Chaetomorpha auricoma*. However, questions still exist as to the conspecificity of Suhr's *Conferva auricoma* and Areschoug's *Conferva cannabina*. At present, specimens of *C. auricoma* Suhr have not been examined. Specimens of *Conferva cannabina* Areschoug, distributed in Alg. Scand. Exsicc. (1840; #14) were examined through the courtesy of the Riksmuseet (S) and Rijksherbarium (L) and represent a remotely branched member of the Cladophoraceae. However, until type material of *Conferva auricoma* Suhr can be examined, the proper generic placement and specific classification of the two species must be reserved. It should be noted that the herbarium specimens examined from various institutions identified as *Chaetomorpha cannabina* were referable to either *Chaetomorpha brachygona* or *Rhizoclonium tortuosum*, and none fit the description attributed to *C. cannabina*. Concern about possible conspecific relationships existing between some of the more narrow *Chaetomorpha* and *Rhizoclonium* species have previously been noted (p. 197).

Finally, with regard to the separation of the genera *Chaetomorpha* and *Rhizoclonium*, a review of the characters used to separate the two genera shows none of the characters to be valid criteria. The names *Rhizoclonium* and *Chaetomorpha* bring forth specific thoughts of shape and form for many taxonomists. However, the characters that have been used to separate the genera have been shown to be erroneous criteria or based on environmentally

variable characteristics. The genus *Rhizoclonium* was originally described with a single sentence "*Trichomata parenchymatica, coelogonimica, ramus verticales, radicoutes emittentis*" (Kützing, 1843). The description of *Chaetomorpha* (Kützing, 1845) was not much more elaborate but did point out the unbranched nature of the plant, and that it was a uniseriate filament with laminated cells that were as long as broad or longer, but less than 4 times the width.

Previous authors have employed various characters to differentiate the genera: cell shape (Collins, 1909; Setchell & Gardner, 1920), mode of attachment (Bold & Wynne, 1978; Abbott & Hollenberg, 1976; Taylor, 1957; Setchell & Gardner, 1920; Collins, 1909), and number of nuclei per cell (Setchell & Gardner, 1920). The most common criterion for separation of the genera has been mode of attachment, with basal holdfasts in *Chaetomorpha* and rhizoids in *Rhizoclonium*. However, past studies have shown *Rhizoclonium* species to have basal holdfast stages at some point in their life history (*R. tortuosum:* Perrot, 1965; *R. riparium* (= *R. implexum*) (Dillw.) Küt. : Nienhuis, 1975). The presence or absence of rhizoids has also been used as a diagnostic character for delineation of *Rhizoclonium*. Nienhuis (1975) and Patel (1971b) have shown rhizoidal proliferation and complexity to be affected by light intensity, substratum firmness, light quality, and temperature. The demonstrated variability of this character, and the fact that the New England populations of *R. tortuosum* often lack rhizoids, makes this character of little use in generic separation.

Chapman (1939) cited the width of the filament as the distinguishing character between the species. The original description of the genera, however, gave no dimensional characteristics. Further, a continuum of cell widths is present between *Chaetomorpha* and *Rhizoclonium* (Table 2). Other criteria, such as pyrenoid number and number of nuclei per cell, have been shown to vary with the cell volume and are not specific or generic indicators in the unbranched Cladophoraceae (Prasad, et al., 1973; Price, 1967; Carter, 1919).

It appears then, that the question must be raised as to the continued separation of the two genera, at least on the basis of traditional characteristics. Further information reflecting the close relationship between these two groups can be seen in the chromosome numbers of the species within the genera (Table 3). As stated by Sinha (1953), there appears to be a polyploid series with a base

Table 2. **Cellular dimensions of representative species of *Chaetomorpha* and *Rhizoclonium***

SPECIES	CELL WIDTH	CELL LENGTH
Rhizoclonium riparium (Nienhuis, 1975)	8 to 48 μm	1 to 4 times the width
Chaetomorpha minima (Taylor, 1960 & present study)	10 to 40 μm	1 to 2 times the width
R. tortuosum (= *Lola tortuosa*) (present study)	27 to 75 μm	2 to 3 (1–4) times the width
Chaetomorpha brachygona (present study)	75 to 150 μm	1 to 2 times the width
C. linum (present study)	150 to 450 μm	0.75 to 1.5 times the width

Table 3. **Chromosome numbers of various *Chaetomorpha* and *Rhizoclonium* species**

SPECIES	2*n*	1*n*	AUTHOR
Rhizoclonium riparium	36	18	Sinha (1958)
R. tortuosum	24	—	Sinha (1958)
	22	—	Patel (1971b)
	20	10	Perrot (1965)
Chaetomorpha linum	36	18	Patel (1971a)
	36	18	Sinha (1958)
C. aerea	24	12	Patel (1971a)
	20	10	Hartman (1929)
C. melagonium	24	12	Patel (1972)

number of 6. Although enough information is available at present to question the validity of generic separation, additional information concerning the remaining species of *Chaetomorpha* and *Rhizoclonium* must be collected before the final disposition of the two genera is made.

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LITERATURE CITED

ABBOTT, I. A., & G. J. HOLLENBERG. 1976. Marine algae of California. Stanford University Press. Stanford.

AGARDH, C. A. 1824. System algarum. Lund.

AGARDH, J. G. 1842. Algae maris mediterranei et Adriatici. Parisiis.

ARESCHOUG, J. E. 1840. Algae scandinavicae exisccatae.

_____. 1843. Algarum (Phycearum) minus rite congnitarum pugillus secundus. Linnaea. p 268.

_____. 1850. Phycearum quae in maribus Scandinaviae Cresent, enumerato, sectic posterior ulvacaes contrien. Nov. Acta Reg. Soc. Sci. Uppsala. **14:** 432 433.

BLAIR, S. M. 1978. Biosystematic and taxonomic investigations of selected species of *Rhizoclonium* Kützing and *Chaetomorpha* Kützing in New England. M.S. Thesis, University of New Hampshire. Durham.

_____., A. C. MATHIESON, & D. P. CHENEY. 1982. Morphological and electrophoretic investigations of selected species of *Chaetomorpha* (Chlorophyta; Cladophorales). Phycologia **21:** 164–172.

BOLD, H. C., & M. J. WYNNE. 1978. Introduction to the algae: structure and reproduction. Prentice-Hall Inc. Englewood Cliffs.

BØRGESEN, F. 1925. The marine algae from the Canary Islands I. Chlorophyceae. K. Danske Vidensk. Selsk. Biol. Medd. **5:** 1 123.

CARTER, N. 1919. The cytology of the Cladophoraceae. Ann. Bot. **33:** 476 478.

CHAPMAN, V. J. 1939. Some algal complexities. Rhodora. **41:** 19–28.

CHRISTENSEN, T. 1957. *Chaetomorphia linum* in the attached state. Bot. Tidsskr. **53:** 311–316.

_____. 1975. Annotations to a distribution survey of Danish marine algae. Bot. Tidsskr. **69:** 253 256.

COLLINS, F. S. 1909. The green algae of North America. Tufts Coll. Stud. Vol. 2 no. 3.

———. 1918. The green algae of North America. Second supplement. Pap. Tufts Coll. Stud. — Sci. Ser. no. **37.**

———, & A. B. Hervey. 1917. The algae of Bermuda. Pro. Am. Acad. Arts Sci. **53:** 3 195.

Dillwyn, L. W. 1809. Synopsis of British Confervae. London.

Edelstein, T., & J. McLachlan. 1967. Investigations of marine algae of Nova Scotia IV. Species of Chlorophyceae new or rare to Nova Scotia. Can. J. Bot. **45:** 211 214.

Farlow, W. G. 1881. The marine algae of New England and adjacent coast. Report U.S. Fish. Comm. for 1879.

Hamel, G. 1929. Heterogamy of Cladophoraceae *Lola* (gen. nov.) *lubrica* (Setch. & Gard.) C.r. hebd. Seanc. Acad. Sci., Paris **189:** 1904–1906.

Hartman, M. 1929. Untersuch urger uber die Sexualitat und den Generationswechsel von *Chaetomorpha* und *Entermorpha*. Ber. It. bot. Ges. **47:** 485–494.

Harvey, W. H. 1846-51. Phycologia Brittanica. Vol. IV.

———. 1857. Neris Boreali-Americana: Part III.

Holmgren, P. K. & K. Keuken. (Ed.) 1974. Index Herbariorum I: The herbaria of the world. Regnum veg. Vol. **92.**

Kjellman, F. R. 1883. The algae of the Arctic Sea. Kongl. Sv. Vet-Akad. Handl. **20:** 312.

———. 1889. Om Beringhafuets Algflora. Kong. Sv. Vet.-Akad. Handl. **23**(8): 58 pp, 7 pls.

Kornmann, P. 1972. Ein Beitrag zur Taxonomie der Gattung Chaetomorpha (Cladophorales, Chlorophyta). Helgolander wiss. Meeresunters **23:** 1–31.

———, & P. H. Sahling. 1977. Meeresalgen von Helgoland. Helgolander wis. Meeresunter **29:** 1–289.

Koster, J. T. 1955. The genus *Rhizoclonium* in the Netherlands. Publ. Sta. Zool. Naples, Italy. **27:** 335 357.

Kützing, F. T. 1843. Phycologia generalis. Leipzig.

———. 1845. Phycologia germanica. Nordhausen.

———. 1847. Diagnosen und Vernerdugensuneyen oder dritischen algen. Bot. Ziet. Vol. **5.**

———. 1849. Species algarum. Liepzig.

———. 1853. Tabulae phycologicae. Nordhausen. Vol. 3.

Linneaus, C. 1753. Species Plantarum. Vol. 2. Holmiae.

Mazé, H., & A. Schramm. Essai de classification des algue de la Guadeloupe. Second edition. Basse Terre.

Montagne, J. E. C. 1849. Sixième centurie de plantes cellulaires nouvelles, tant indigènes qu'exotiques. Decades III à IV. Ann. Sci. Nat. 3 ser. Bot. **11:** 33–66.

Müller, O. F. 1778. Icones Plantarum sponte nascentium in regris Davie et Norvegie et in Ducatibus slesvici. Holsatiae et Olbeburg, ad illustrandum opus de iisdem plantis, regio jussu esarandum. Florae Danicae **5:** 721–780.

Nienhuis, P. H. 1975. Biosystematics and ecology of *Rhizoclonium riparium* (Roth) Harvey (Chlorophyceae: Cladophorales) in the estuarine area of the rivers Rhine, Meuse, and Scheldt. Rotterdam.

Patel, R. J. 1971a. Cytotaxonomical studies on *Chaetomorpha* I. *Chaetomorpha linum* (Müll) Küt. and *C. aerea* (Dillw). Küt. Phykos **11:** 17 22.

———. 1971b. Cytotaxonomical studies on *Rhizoclonium* spp. 1. *Rhizoclonium implexum* (Dillw.) Küt. Seaweed Res. Util. **1:** 8 18.

———. 1972. Cytotaxonomical studies of British marine species of *Chaetomorpha* II. *Chaetomorpha melagonium* (Web. *et* Mohr) Küt. Phykos **11:** 17–22.

Perrot, Y. 1965. Sur le cycle de reproduction d'une Cladophoracee marine de la région de Roscoff: *Lola implexa* (Harvey). C.r. hebd. Seanc. Acad. Sci., Paris. **261:** 503 506.

Prasad, B. N., S. Dutta, & V. Jain. 1973. Cytological studies in the genus *Rhizoclonium hieroglyphicum*. Phykos **12:** 106 113.

Price, W. M. 1967. Some aspects of the biology and taxonomy of the unbranched Cladophorales in the British Isles. Thesis, University of Liverpool.

Roth, A. G. 1797. Catalecta botanica plantae novae it minus cognitae discribunter atque illustrantur. Fasc. 1.

Scagel, R. F. 1966. Marine algae of British Columbia and northern Washington. Part I: Chlorophyceae. National Museum of Canada. Bulletin **207.** Biol. Ser. 74.

Setchell, W. H., & N. L. Gardner. 1920. The marine algae of the Pacific coast of North America. Part 2, Chlorophyceae. Univ. Calif., Berkeley. Publ. Bot. **8:** 139–374, pls. 9–33.

Silva, P. C. 1950. Generic names of algae proposed for conservation. Hydrobiologia **2:** 252 280.

Sinha, J. P. 1958. Chromosome numbers and life cycles in members of Cladophorales. Br. Phyco. J. **1:** 24 27.

Stafleu, F. A. (Ed.) 1978. International Code of Botanical Nomenclature. Regnum veg. Volume **97.**

Stockmayer, S. 1898. Uber die Algengattung *Rhizoclonium*. Verh. Zool.-bot. Ges. Wien. **40:** 571.

Suhr, J. N. 1840. Bietrage zur Algen Kunde. Flora **40:** 289 320.

Taylor, W. R. 1937a. Notes on North Atlantic Marine algae. Pap. Mich. Acad. Sci. **22:** 225 233.

———. 1957. The marine algae of the northeast coast of North America. Univ. of Mich. Press. Ann Arbor.

———. 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. Univ. Mich. Press. Ann Arbor.

Vickers, A. 1905. List des alg. mar. de la Barbade. Ann. Sci. Nat. Bot **9:** 45 66.

Weber, F., & D. M. H. Mohr. 1804. Naturhistorische Reise durch einen Teil Schwedens. Göttingeal.

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"*Kalmia ericoides* revisited."

A block of text, comprising lines 4 16 on page 52 as published, was transposed from page 54. The mislocated text should start as line 5 of page 54, continuing the description and Distribution & Ecology sections of the discussion of *Kalmia ericoides* Wright ex Griseb. var. *aggregata* (Small) Ebinger.

ANATOMY OF THE PERICARP OF CLIBADIUM, DESMANTHODIUM AND ICHTHYOTHERE (COMPOSITAE, HELIANTHEAE) AND SYSTEMATIC IMPLICATIONS

TOD F. STUESSY AND HO-YIH LIU

ABSTRACT

The closely related genera, *Clibadium*, *Desmanthodium*, and *Ichthyothere* (Compositae, Heliantheae) are distributed in Mexico, Central America, and Northern and Central South America. Some of the species of *Clibadium* (e.g., *C. laxum*) have drupaceous achenes, which is unusual in the family. Comparative anatomical studies of fruits of the three genera show a strong similarity in the arrangement of the epidermis, hypodermis, and phytomelan and fiber layers. In most regards, *Desmanthodium* and *Ichthyothere* are more similar to each other than either is to *Clibadium*. The method of deposition of the phytomelan in all three genera begins with a series of tubes and cones from the fiber layer followed by patchy deposition of dark resistant material that eventually solidifies into a continuous layer. The phytomelan layer probably functions to protect the developing embryo and may also serve in regulating timing of germination.

The genus *Clibadium* L. of the Compositae (tribe Heliantheae), with 30–40 species ranging from Mexico to Peru, is unusual among members of the family in that some species have drupaceous achenes. Only two other genera of the family are known to have similar fleshy fruits (Huber, 1898; Norlindh, 1977): *Chrysanthemoides* Tourn. ex. Fabr. (tribe Calenduleae) and *Wulffia* Neck. ex Cass. (Heliantheae). Because *Clibadium* has already been studied for flavonoids (Bohm & Stuessy, 1981a), for sesquiterpene lactones and polyacetylenes (Czerson, et al., 1979), and for chromosome numbers and morphology for an eventual systematic synthesis by the senior author, an investigation of the anatomy of the unusual fruits of *Clibadium* would seem helpful. Especially useful would be indications of possible subgeneric groupings to test the sectional classification of Schulz (1912) and to compare with the broad flavonoid differences documented recently (Bohm & Stuessy, 1981a).

Clibadium is closely related to *Desmanthodium* Benth., which has eight species from Mexico and Central America, and to *Ichthyothere* Mart., with 15 species in South America, especially Brazil (Stuessy, 1977). Although the achenes of these other two genera are not known to be fleshy, a comparative examination of fruit anat-

omy would be useful to provide clues to evolutionary relationships both within and among all three taxa. This is especially important because the senior author (1977) has judged the three genera to be closely related (all placed in subtribe Milleriinae) whereas Robinson (1978, 1981) has recommended that each be placed in a separate subtribe (Clibadiinae, Desmanthodiinae, and Melampodiinae) of the Heliantheae. In addition, our preliminary studies on the pericarp of *Clibadium* provided some insights on the method of formation of the stony phytomelan layer. This dark brown or black layer is known to occur in the Compositae, primarily in the tribes Eupatorieae and Heliantheae (Hanausek, 1912; Vaughan, 1970; Misra, 1972; Wagenitz, 1976; Hegnauer, 1977). It was hoped that understanding the initiation and development of the phytomelan layer in the three genera, therefore, might provide even further insights to their evolutionary affinities as well as help reveal the mode of deposition of the phytomelan layer itself. A number of studies have been done on the origin of this layer in the Compositae (Hanausek, 1902, 1907, 1912; Vries, 1948; Politis, 1957; Misra, 1964, 1972; Pullaiah, 1979, 1981), but they have been inconclusive as to events that result in its formation.

The purposes of this paper, therefore, are to: (1) examine the achenial anatomy of different species within *Clibadium*, *Desmanthodium*, and *Ichthyothere* to learn if subgeneric groupings might be suggested within each; (2) postulate evolutionary relationships among the three genera based on pericarp anatomy; and (3) gain some insights on the development of the phytomelan layer in all three genera.

MATERIALS AND METHODS

Nineteen species of *Clibadium* (38 populations), three of *Desmanthodium* (five populations) and eight of *Ichthyothere* (11 populations) were examined (Table 1). Preparation of the achenes for studying the outer surface of the phytomelan layer was accomplished by soaking in 10% NaOH for 4–14 hours followed by mechanical removal of the outer pericarp and finally by washing in distilled water. A few preparations were soaked in dilute HCl for one hour and then washed. This surface was then shadow-coated with gold and viewed in the SEM.

Table 1. Voucher specimens of taxa of *Clibadium*, *Desmanthodium*, and *Ichthyothere* examined by SEM for external surface of the phytomelan layer and by light microscopy for pericarp anatomy. All vouchers cited here and elsewhere in this paper are at OS unless indicated otherwise (herbarium acronyms in parentheses after Holmgren, Keuken, and Schofield, 1981).

SF = Stuessy & Funk; *SG = Stuessy & Gardner*; *SJ = Stuessy & Jansen*; *SN = Stuessy & Nesom.*

F = freehand sections; P = paraffin-embedded sections; SEM = external SEM observations; SS = serial sections.

Taxa and Vouchers

Clibadium *anceps* Greenm., *SG 4518* [P,SS], *Wilbur & Stone 10678* [SEM]; *C. arboreum* J.D. Smith, *Dwyer 11415* [SEM], *SG 4574* [F, SEM]; *C. asperum* (Aubl.) DC., *Castañeda 6144* (NY) [SEM], *Killip & Smith 26834* (GH) [SEM], *McDaniel 2366* (US) [SEM], *SN 5899* [SEM]; *C. glomeratum* Greenm., *SG 4517* [SEM, SS]; *C. grandifolium* S.F. Blake, *Gentry 3034* [SEM], *SG 4533* [P,SS]; *C. laxum* S.F. Blake, *SJ 4942* [P, SEM, SS]; *C. leiocarpum* Steetz in Seem., *Almeda & Nakai 10678* [SEM], *SG 4456* [F]; *C. micranthum* O.E.Schulz, *Killip & Smith 24822* (NY) [SEM]; *C. parviceps* S.F. Blake, *Williams 10478* (US) [SEM]; *C. pentaneuron* S.F. Blake, *Pelaéz 510* (US) [SEM] *SF 5709* [SS]; *C. peruvianum* Poepp. ex DC., *Killip & Smith 27263* (US) [SEM], *Mexia 6506a* (NY) [SEM]; *C. pilonicum* Stuessy, *Hartman 3963* [SEM]; *C. pittieri* Greenm., *Cuatrecasas 13709* (US) [SEM], *Forero & Gentry 725* (COL) [SEM], *Standley 45815* (US) [SEM], *SG 4465* [SS]; *C. psilogynum* S.F. Blake, *Weberbauer 7864* (GH) [SEM]; *C. sessile* S.F. Blake, *Hartman 3916* [SEM]; *C. sprucei* S.F. Blake, *SN 4811* [SS]; *C. surinamense* L., *Bristor 690* (US) [SEM], *Cuatrecasas 14004* (US) [SEM], *SG 4451* [SEM], *SN 5856* [SS], *SPJ 4935* [SEM]; *C. terebinthinaceum* DC., *Cuatrecasas 23932* (F) [SEM], *Fuchs et al. 21728* (COL) [SEM], *SF 5737* [F]; *C. trianae* S.F. Blake, *Cuatrecasas 6475* (F) [SEM], *SN 4680* [F].

Desmanthodium *fruticosum* Greenm., *King & Soderstrom 505* (UC) [SEM], *SG 4115* [P, SEM, SS]; *D. hondurense* A. Molina, *Hazlett 849* (MO) [SEM], *SG 4390* [SS]; *D. perfoliatum* Benth., *SG 4306* [F, SEM].

Ichthyothere *agrestis* Baker in Mart., *Hatschbach 19911* (F) [F]; *I. cordata* Malme, *Maguire & Maguire 44510* (NY) [F]; *I. cunabi* Mart. in Buchn., *Dusén s.n.* (MO) [F]; *I. hirsuta, Irwin et al. 25876;* (MO) [SS]; *I latifolia* Gardn., *Irwin et al. 34716* (MO) [F]; *I. rufa* Gardn., *Argent 6711* (NY) [SEM]; *I scandens* S.F. Blake, *Cuatrecasas 13313.* (COL) [F]; *I. terminalis* (Spreng.) Malme, *Assis 157* (UC) [SS], *Forero, Bastidas & Ramírez 882* (NY) [P, SS], *Pereira 7535* (NY) [P, SEM, SS], *Prance 8603* (NY) [SEM].

Sections of pericarp were made free-hand and by traditional paraffin embedding and sectioning (Sass, 1958). Stains used for the paraffin mounts were safranin and fast green. The serial sections were done in all paraffin material plus 12 other collections (Table 1) cut free-hand to determine the degree of constancy of pericarp anatomy throughout the achene.

RESULTS

Structure of Pericarp

The anatomy of the pericarp in *Clibadium*, *Desmanthodium*, and *Ichthyothere* is basically similar with five distinct zones observable (Fig. 1–6): epidermis, hypodermis, phytomelan layer, fiber zone, and internal parenchyma. Within each genus a constancy of anatomical features exists among the species examined. In addition, the organization of the pericarp is constant throughout the entire length of the achene. Slight variations occur in numbers of hypodermal cell layers and thickness of the phytomelan layer, but they are minor and do not obscure nor contradict patterns observed and documented (Figs. 1–6; Table 2).

The pericarp is the thickest in *Clibadium*, with *Ichthyothere* next, followed by *Desmanthodium*. The species of *Clibadium* with drupaceous fruits (such as *C. laxum*) are such due to an inflated hypodermis with more and larger cells and cell layers. In all other respects they have the same structure as the other species of the genus with dry achenes. The epidermis and internal parenchyma provide no significant taxonomic characters for differentiating the three genera. The hypodermis, however, does differ, with parenchyma being 2–5 cells thick and radially arranged in *Clibadium* and 3–6 cells thick and irregularly arranged in *Ichthyothere*. *Desmanthodium* has only 1–2 parenchyma cell layers. The phytomelan layer is different in the three genera (Figs. 1–3; Table 2), and this is

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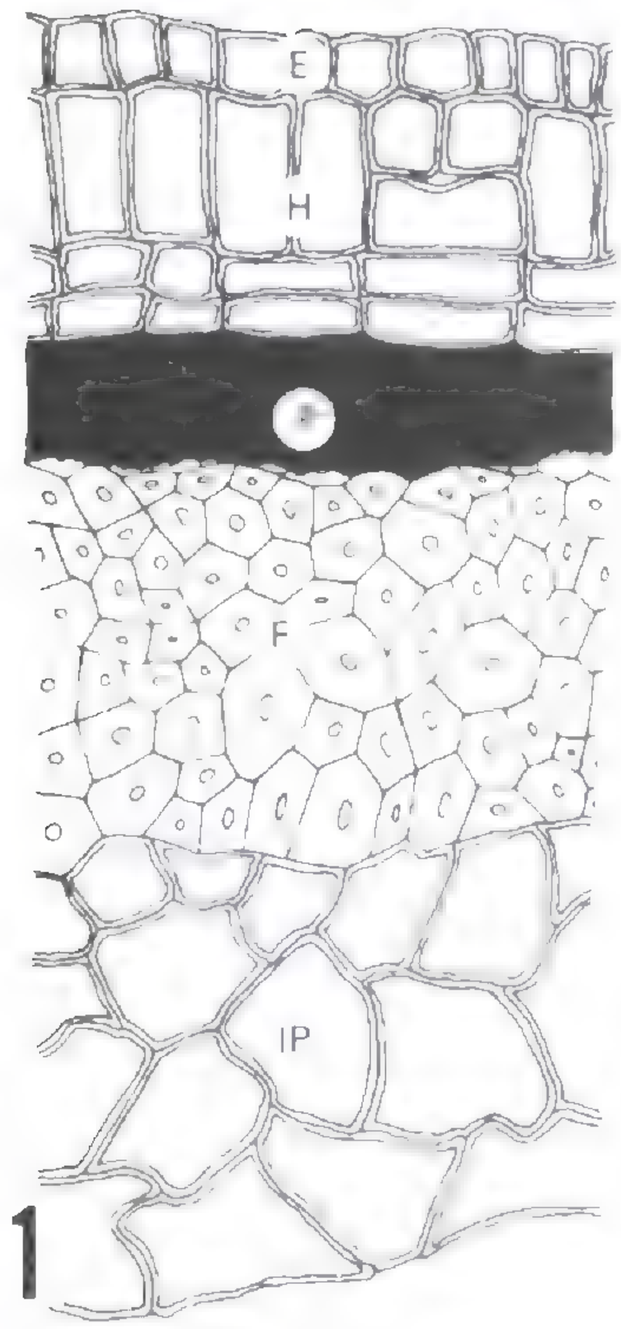
Figures 1–6. Transections of mature (Fig. 1–3) and immature (4–6) pericarps of *Clibadium*, *Desmanthodium*, and *Ichthyothere*. **1.** *C. laxum*, *SJ 4942*. **2.** *D. fruticosum*, *SG 4115*. **3.** *I. terminalis*, *Pereira 7535* (NY). E, epidermis; H, hypodermis; P, phytomelan layer; F, fiber zone; IP, internal parenchyma.



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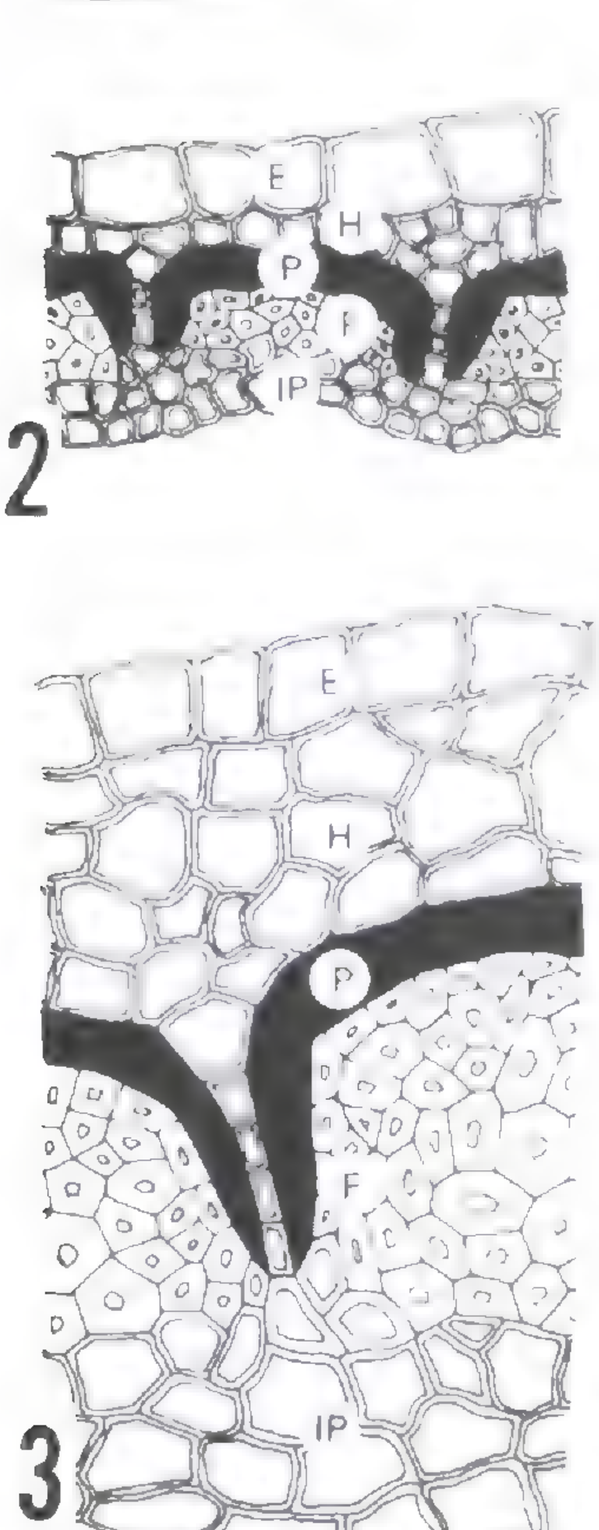

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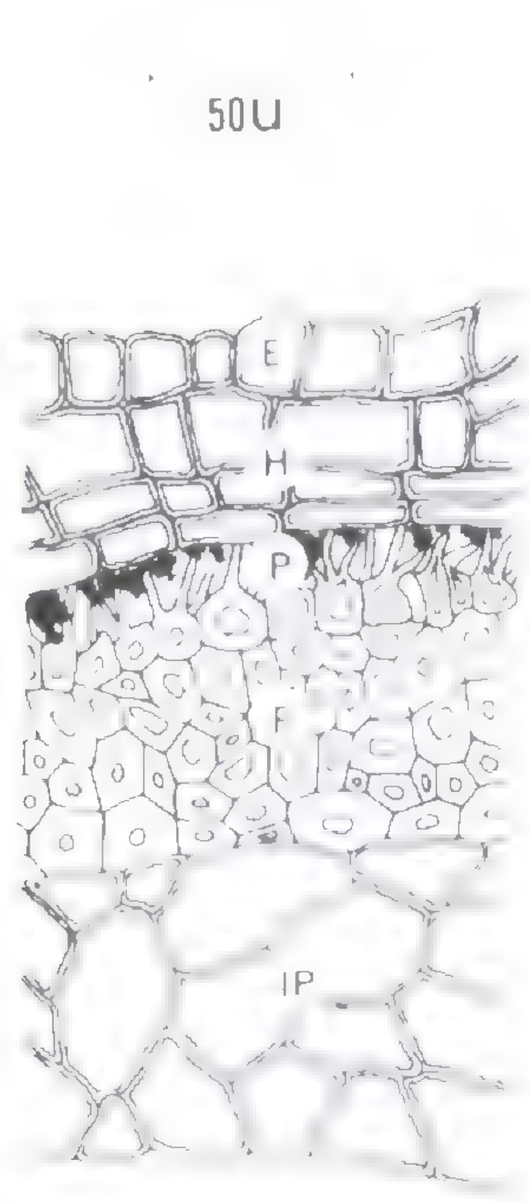

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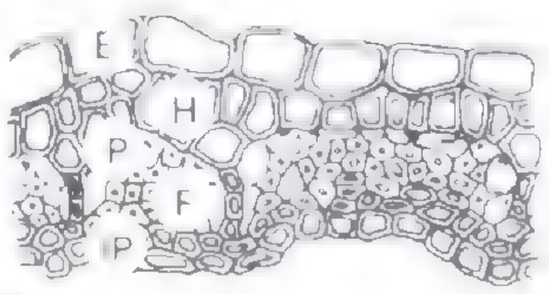

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Table 2. Comparison of pericarp anatomy in *Clibadium*, *Desmanthodium*, and *Ichthyothere*.

Region of pericarp	*Clibadium*	*Desmanthodium*	*Ichthyothere*
Hypodermis	2–5 cell layers of parenchyma in radial files	1–2 cell layers of parenchyma	3–6 cell layers of parenchyma irregularly arranged
Phytomelan layer	continuous and regular	discontinuous, associated with fiber bundles	discontinuous, associated with fiber bundles
Fiber zone	continuous, 4–10 cell layers thick	discontinuous, bundles of 15–55 fibers	discontinuous, with large (70–140) and small (20–40) bundles of fibers

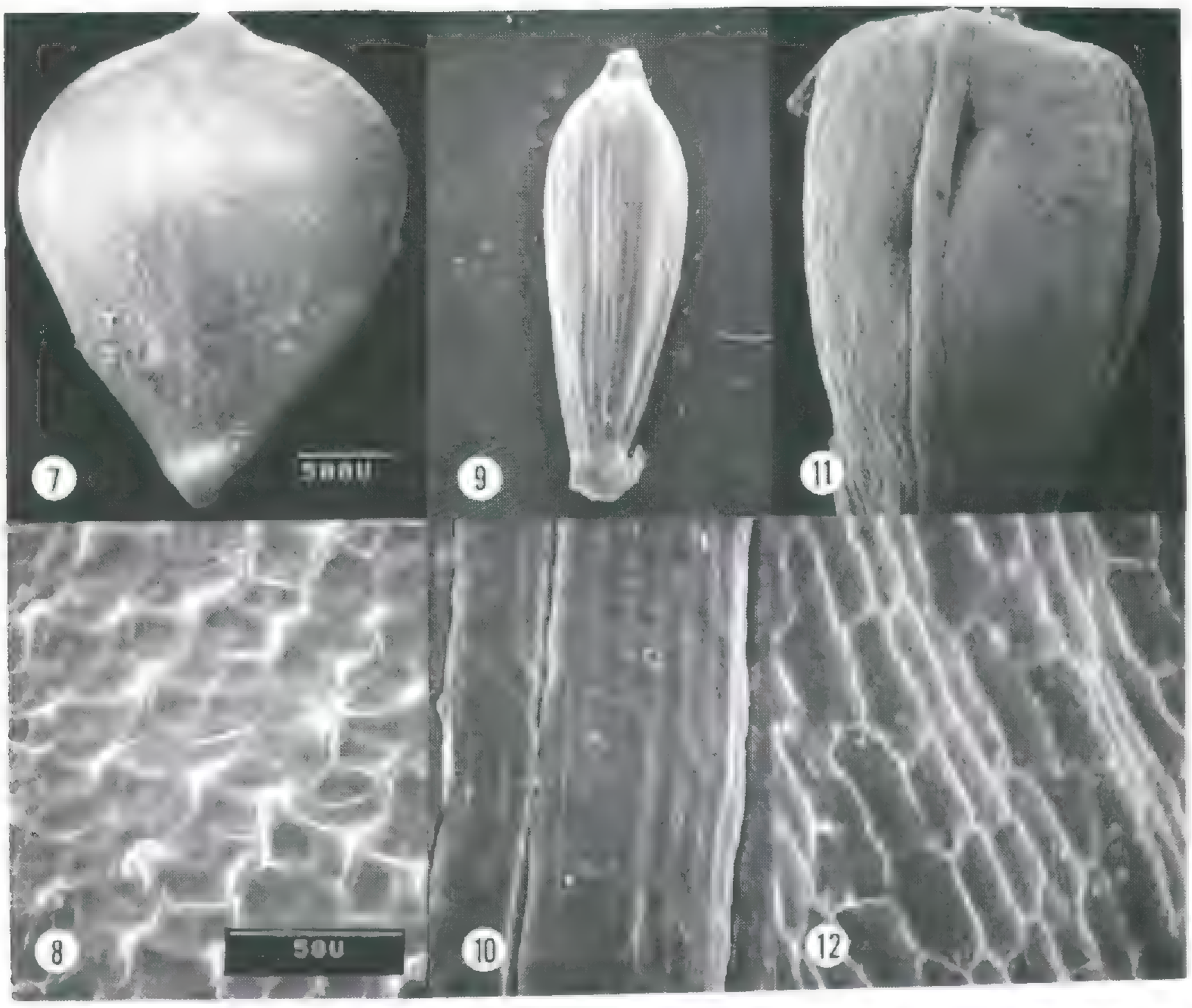
especially evident in surface configuration (Figs. 7–12). *Clibadium* has a thick continuous phytomelan layer, *Ichthyothere* has the layer interrupted by eight longitudinal grooves, and *Desmanthodium* has numerous longitudinal grooves over the entire surface of the achene. In all taxa the phytomelan is intimately associated with the fiber zone immediately below. The fibers appear similar in the three genera, but in *Clibadium* they form a continuous layer (as with the phytomelan), in *Ichthyothere* the fibers are interrupted eight times, and in *Desmanthodium* they are interrupted many times resulting in numerous small clusters.

Variations in Upper Surface of Phytomelan Layer

The upper surface of the phytomelan in *Clibadium*, *Desmanthodium*, and *Ichthyothere* differs at the generic level with *Desmanthodium* being nearly smooth and the former and the latter having more regular cellular sculpturing (Figs. 7–12). These cellular patterns result from the formation of phytomelan against the cells of the hypodermis; the phytomelan itself is acellular. Within each genus, minor variations of sculpturing exist, but they are not significant for the recognition of most species and they also show some developmental variation.

Development of Phytomelan Layer

Examination of cross-sections of young achenes of species of *Clibadium*, *Desmanthodium*, and *Ichthyothere* (Figs. 4–6) reveals general aspects of the system of development of the phytomelan layer. In all three genera the fiber zone below and hypodermis above serve as templates between which the phytomelan begins to be deposited. A developmental sequence in *Clibadium surinamense* serves as an example for these details (Figs. 13–18). The upper cell layer of the fiber zone has tubular or cone-shaped extensions (Figs. 4 & 13), which touch the hypodermis. It is not clear whether the phytomelan derives from the fiber zone, the hypodermis, or both. The phytomelan thickens and fuses laterally (Figs. 14–16), and eventually forms a hardened solid layer (Figs. 17 & 18). *Ichthyothere* and *Desmanthodium* develop in a similar fashion (Figs. 5, 6, 19, & 20 for similar early stages).



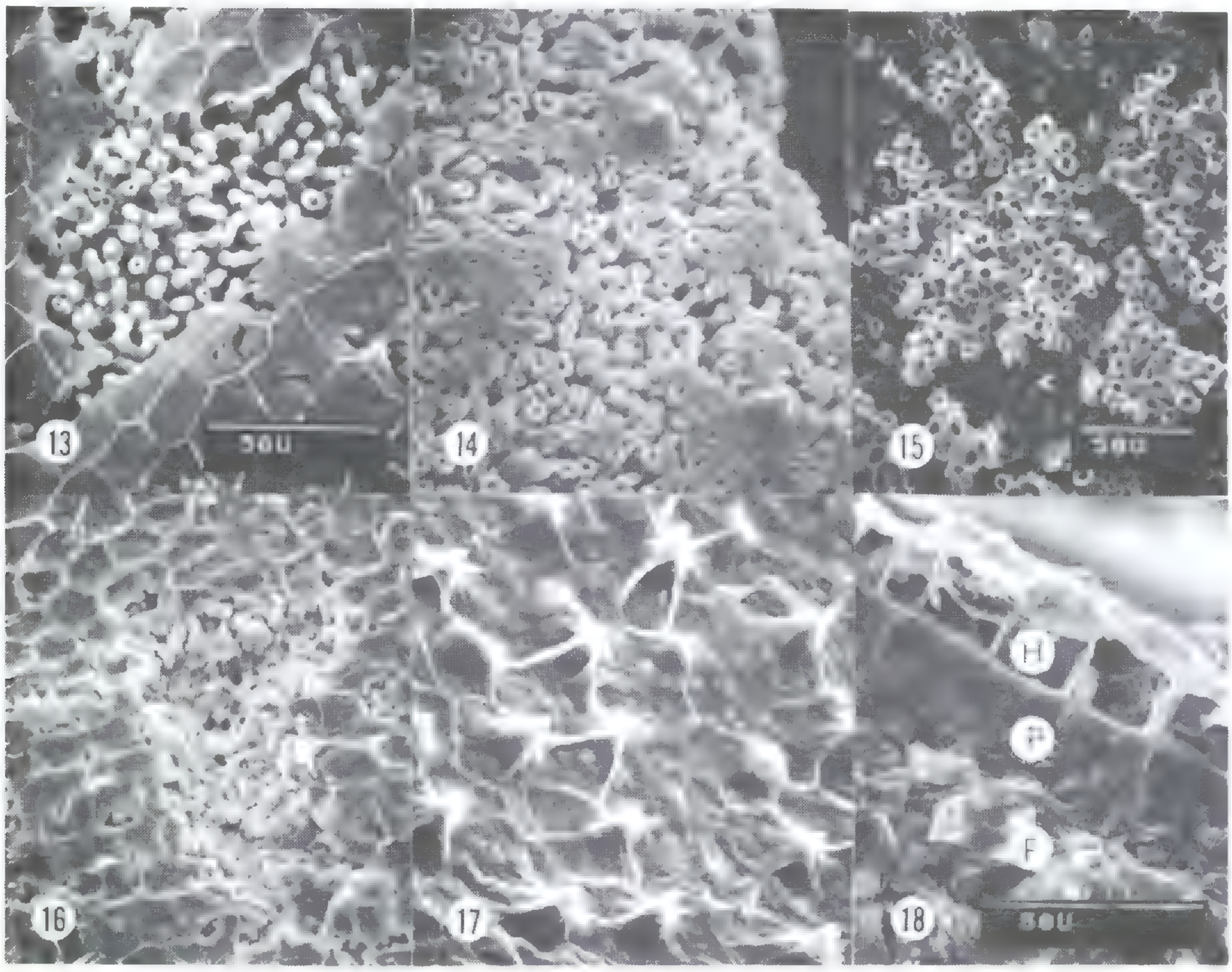
Figures 7–12. External surface of phytomelan layer of mature achenes of *Clibadium*, *Desmanthodium*, and *Ichthyothere*. **7 & 8.** *C. pittieri, Standley 45815* (US). **9 & 10.** *D. fruticosum, King & Soderstrom 5058* (UC). **11 & 12.** *I. rufa, Argent 6711* (NY). All scale as in Figs. 7 & 8.

DISCUSSION

Systematic and Evolutionary Significance of Variations in Pericarp Structure

Because of the initial interest in the unusual drupaceous achenes of some species of *Clibadium*, it was hoped that many differences in pericarp structure would be found *among* species of the genus. Although some minor variations do occur (e.g., a more elevated series of tubercles on the upper surface of the phytomelan layer in *C. sychnocephalum*), they are not generally useful at either the specific or subgeneric levels within any of the genera.

The differences in pericarp structure among the three genera, however, are significant and help distinguish them more clearly (cf. differences listed in Table 2). A more important question is how

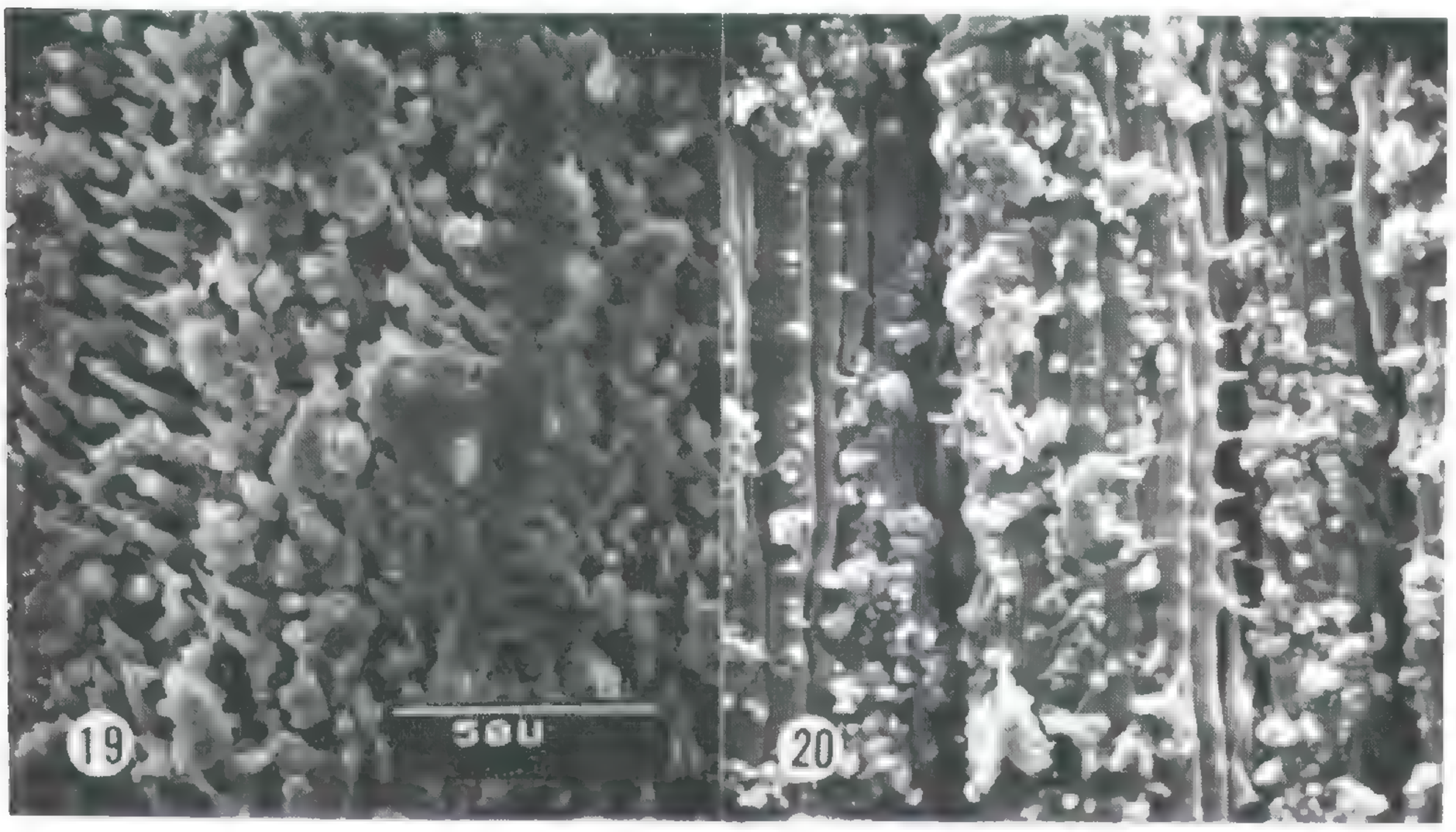


Figures 13–18. Development of phytomelan layer in *Clibadium surinamense*. **13.** Surface of very immature achene with hypodermis partially removed, showing tubular extensions of fibers (FAA preservation). **14.** Surface of young achene with hypodermis completely removed showing initiation of phytomelan around tips of extensions (FAA preservation. NaOH cleaning). **15.** Inner view of hypodermis showing attachment of upper part of extensions with beginnings of envelopment by phytomelan and extensions fractured below (dry). **16.** Surface of nearly complete and phytomelan layer (dry). **17.** Surface of mature phytomelan layer (dry, with NaOH cleaning). **18.** Transection of mature achene wall (dry) with solid phytomelan layer (P) between hypodermis (H) and fibers (F) below; compare with Fig. 1. Figs. 13, 15, 16, 18, *Stuessy & Gardner 4451*; 14, *Stuessy et al, 4935*; 17, *Bristor 690* (US). Figs. 13, 14, & 17, and 15 & 16 same scales, respectively.

closely related the three genera are to each other. The structure and development of the pericarp is essentially the same and suggests a strong evolutionary tie. Particularly noteworthy are the extensions of the fibers around which the phytomelan accumulates. Although a number of Compositae have been analyzed for pericarp features (Hanausek, 1902, 1912; Briquet, 1916; Giroux, 1930, 1933; Vries, 1948; Misra, 1964, 1972; Carlquist, 1958; Dittrich, 1968a, b, 1969), it remains to be seen how relatively close *Clibadium, Desmantho-*

dium, and *Ichthyothere* will be after many other genera of the Heliantheae are investigated. Nonetheless, the similarity of pericarp features does not appear to support Robinson's (1978, 1981) placement of *Clibadium*, *Desmanthodium*, and *Ichthyothere* in separate subtribes.

The strong similarities of pericarp structure in *Clibadium*, *Desmanthodium*, and *Ichthyothere* make it difficult to determine the relationships of the genera one to another. The most significant point seems to be that *Desmanthodium* and *Ichthyothere* are similar in having discontinuous phytomelan as opposed to it being continuous in *Clibadium*. This suggests that the two are more closely related than either is to *Clibadium*. On the other hand, the similar cellular patterns of the external phytomelan surface in *Clibadium* and *Ichthyothere* argue for their close relationship, in contrast to the smooth surface in *Desmanthodium*. The ontogeny of the phytomelan layer in all three genera is essentially the same, except that *Desmanthodium* and *Ichthyothere* have more conical and smaller fiber extensions whereas those in *Clibadium* are larger and more tubular.



Figures 19 & 20. Surface of young achene showing patchy development of phytomelan layer in *Ichthyothere terminalis* (**19**. dry, NaOH cleaning; *Prance et al. 8603*, NY) and *Desmanthodium perfoliatum* (**20**. FAA, HCl cleaning, *Stuessy & Gardner 4306*). Same scale.

Studies on the structure and development of the pericarp do not indicate which type is the most evolutionary primitive and which is more advanced. Because of the absence of comprehensive studies on genera of the Heliantheae, the basic pattern in the tribe is not yet known. This makes evolutionary directionality difficult to determine. One might speculate that the structure of *Clibadium* may be more primitive simply because it is a more simple pattern. Chromosome numbers give limited support to this idea because *Clibadium* is known as $n = 16$ and 24 (x = probably 8) (Turner & King, 1964; Coleman, 1968; Powell & King, 1969a, b; Powell & Cuatrecasas, 1970; Grashoff, Bierner, & Northington, 1972; Solbrig, et al., 1972), *Desmanthodium* as $n = 18$ (Fay, 1974; Keil & Stuessy, 1977), and *Ichthyothere* as $n = 32$ (Coleman, 1970). An ancestral base of $x = 8$ for the entire complex is the simplest explanation for these data which would make *Clibadium* and *Desmanthodium*, as the lowest level polyploids, more primitive than the others (*Desmanthodium* may have arisen by polyploidy from an $x = 9$ ascending aneuploid line). The flavonoid data give some suggestion that *Clibadium* has a more primitive biochemical profile than *Desmanthodium*, in that the latter accumulates more mono-, di-, and tri-methyl derivatives (Bohm & Stuessy, 1981b). Alternatively, however, the pattern of phytomelan interrupted by parenchymal rays as in *Desmanthodium* and *Ichthyothere* might be more primitive because this aspect also occurs (Hanausek, 1912; Vries, 1948; Vaughan, 1970) in *Guizotia abyssinica, Helianthus annuus, Madia sativa, Rudbeckia fulgida,* and *Sclerocarpus uniserialis*, taxa of the same tribe (Heliantheae). A continuous layer, however, is also known (Hanausek, 1912) in *Eclipta alba, Engelmannia pinnatifida, Silphium trifoliatum*, and *Verbesina encelioides* of the Heliantheae. More data are obviously needed from many other genera.

Development of Phytomelan Layer

A number of studies on the development of phytomelan in the Compositae exist (e.g., Hanausek, 1902, 1912; Vries, 1948; Politis, 1947; Misra, 1964, 1972; Pullaiah, 1979, 1981). These and our own studies have reported the following observations: (1) the phytomelan forms between the hypodermis and the fiber zone; and (2) the phytomelan is non-cellular, very resistant, and whatever markings or sculpturing it has derives from the hypodermal cell layer in

contact with it (e.g., the tubercles on the phytomelan surface of *Clibadium pittieri* reflect depressions at cell wall junctures of the hypodermis, Figs. 7 & 8). Previous workers (Vries, 1948; Misra, 1964, 1972; Pullaiah, 1979, 1981) have believed the phytomelan to be derived from exudates from the hypodermis. This may be so, but it could not be determined to our satisfaction. Alternatively, material may be exuded from the fiber zone or from both sides of the location of deposition. Detailed cytological and histochemical studies will be needed to resolve this question. The tubes and cones in *Clibadium*, *Desmanthodium*, and *Ichthyothere* may function simply as a framework around and within which the phytomelan solidifies, but they also may transport materials to the site of deposition (this seems especially possible in *Clibadium* with the numerous tubes, more than one would think necessary for just structural purposes; see Fig. 13).

The chemical nature of phytomelan is still unknown although it has been proposed by Dafert and Miklauz (1912) to have a molecular formula $x(C_6H_{10}O_5)\ yH_2O$ and suggested by Hegnauer (1964, 1977) to be a polyacetylene. Our studies show that it is not modified by dilute NaOH or HCl treatment, whereas the cells of the epidermis and hypodermis are easily softened and destroyed.

Likewise, the adaptive value of the phytomelan layer is uncertain, but it probably functions as a protective device for the mature fruit and may also regulate the timing of seed germination. The fact that this layer is found principally within the tribes Eupatorieae and Heliantheae (Hanausek, 1912; Misra, 1972) also gives it special taxonomic potential at the higher levels of the hierarchy in the family. The homologies of structure and developmental patterns will have to be determined before their full efficacy can be appreciated.

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LITERATURE CITED

Bohm, B. A., & T. F. Stuessy. 1981a. Flavonol derivatives of the genus *Clibadium* (Compositae). Phytochemistry **20**: 1053–1055.

_____ ., & _____ . 1981b. Flavonol derivatives of *Desmanthodium* (Compositae). Phytochemistry **20**: 1573–1575.

Briquet, J. 1916. Études carpologiques sur les generes de Composeés *Anthemis*, *Ormenis*, et *Santolina* suivies de quelques conclusiones anatomiques et physiologiques d'interêt général. Ann. Conserv. et Jard. Bot. Genève **19**: 257–313.

Carlquist, S. 1958. Anatomy and systematic position of *Centaurodendron* and *Yunquea* (Compositae). Brittonia **10**: 78–93.

Coleman, J. R. 1968. Chromosome numbers in some Brazilian Compositae. Rhodora **70**: 228–240.

_____ . 1970. Additional chromosome numbers in Brazilian Compositae. Rhodora. **72**: 94–99.

Czerson, H., F. Bohlmann, T. F. Stuessy, & N. H. Fischer. 1979. Sesquiterpenoid and acetylenic constituents of seven *Clibadium* species. Phytochemistry **18**: 257–260.

Dafert, F. W., & R. Miklau'z. 1912. Untersuchungen über die kohleähnliche Masse der Kompositen. Denkschr. kais. Akad. Wiss. Wien, Math.-Nat. Kl. **87**: 143–152.

Dittrich, M. 1968a. Fruchtanatomische und cytologische Untersuchungen an einigen Arten der Gattung *Rhaponticum* Adans. und *Leuzea* DC. (Compositae). Österr. Bot. Z. **115**: 379–390.

_____ . 1968b. Morphologische Untersuchungen an den Früchten der Subtribus Cardueae-Centaureinae (Compositae). Willdenowia **5**: 67–107.

_____ . 1969. Anatomische Untersuchungen an den Früchten von *Carthamus* L. und *Carduncellus* Adans. (Compositae). Candollea **24**: 263–277.

Fay, J. J. 1974. *In*: IOPB chromosome number reports XLV. Taxon **23**: 619–624.

Giroux, M. 1930. Sur la carpologie de quelques Composées Nord-Africaines. Bull. Soc. Hist. Nat. Afr. Nord. **31**: 161–189.

_____ . 1933. Note sur la position systématique des *Chrysanthemum cinerariifolium* (Rev.) Vis. suivi de quelques remarques sur la caractères carpologiques des *Tanacetum*. Bull. Soc. Hist. Nat. Afr. Nord. **24**: 54–62.

Grashoff, J. L., M. W. Bierner, & D. K. Northington. 1972. Chromosome numbers in North and Central American Compositae. Brittonia **24**: 379–394.

Hanausek, T. F. 1902. Zur Entwickelungsgeschicte des Perikarps von *Helianthus annuus*. Ber. Deutsch. Bot. Ges. **20**: 449–454.

_____ . 1907. Die "Kohleschicht" im Perikarp der Kompositen. Sitzungsber. kais. Akad. Wiss. Math.-Nat. Kl., Abt. 1, **116**: 3–32.

_____ . 1912. Untersuchungen über die kohleähnliche Masse der Kompositen. Denkschr. kais. Akad. Wiss. Wien, Math.-Nat. Kl. **87**: 93–142.

Hegnauer, R. 1964. Chemotaxonomie der Pflanzen, Band 3. Birkaüser Verlag, Basel.

_____. 1977. The chemistry of the Compositae, pp. 283 335. *In*: V.H. Heywood, J.B. Harborne, & B.L. Turner (eds.), The Biology and Chemistry of the Compositae. Academic Press, London. (cf. p. 289).

HOLMGREN, P. K., W. KEUKEN, & E. K. SCHOFIELD. 1981. Index Herbariorum, ed. 7. Regnum Veg. **106**: 1 452.

HUBER, J. 1898. Observacoes histologicas e biologicas sobre o fruto da *Wulffia stenoglossa* DC. (Jambú). Bol. Mus. Paraense Hist. Nat. **2**: 96–101.

KEIL, D. J., & T. F. STUESSY. 1977. Chromosome counts of Compositae from Mexico and the United States. Amer. J. Bot. **64**: 791 798.

MISRA, S. 1964. Floral morphology of the family Compositae II. Development of the seed and fruit in *Flaveria repanda*. Bot. Mag. Tokyo **77**: 290 296.

_____. 1972. Floral morphology of the family Compositae V. The seed coat and pericarp in *Verbesina encelioides* (Cav.) Benth. and Hk. f. ex A. Gray. J. Indian Bot. Soc. **51**: 332 341.

NORLINDH, T. 1977. Calenduleae –systematic review, pp. 961 987. *In*: V. H. Heywood, J. B. Harborne, & B. L. Turner (eds.), The Biology and Chemistry of the Compositae. Academic Press, N.Y.

POLITIS, J. 1957. Untersuchungen über die cytologische Bildung der Phytomelane bei einigen *Zinnia*-Arten. Protoplasma **48**: 269–275.

POWELL, A. M. & J. CUATRECASAS. 1970. Chromosome numbers in Compositae: Colombian and Venezuelan species. Ann. Mo. Bot. Gard, **57**: 374–379.

_____., R. M. KING. 1969a. Chromosome numbers in the Compositae: Colombian species. Amer. J. Bot. **56:** 116 121.

_____., & _____. 1969b. Chromosome numbers in the Compositae: West Indian species. Sida **3**: 319 320.

PULLAIAH, T. 1979. Embryology of *Adenostemma, Elephantopus* and *Vernonia* (Compositae). Bot. Notiser **132**: 51 56.

_____. 1981. Studies in the embryology of *Heliantheae* (Compositae). Pl. Syst. Evol. **137**: 203 214.

ROBINSON, H. 1978. Studies in the Heliantheae (Asteraceae). XIV. Validation of subtribes. Phytologia **41**: 39 44.

_____. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithson. Contrib. Bot. **51**: 1–102.

SASS, J. E. 1958. Botanical Microtechnique, ed. 3. Iowa State College Press, Ames, Iowa.

SCHULZ, O. E. 1912. Beiträge zur Kenntnis der Gattung *Clibadium*. Engl. Bot. Jahrb. **46**: 613–628.

SOLBRIG, O. T., D. W. KYHOS, M. POWELL, & P. A. RAVEN. 1972. Chromosome numbers in Compositae VIII: Heliantheae. Amer. J. Bot. **59**: 869–878.

STUESSY, T. F. 1977. Heliantheae –systematic review, pp. 621–671. *In*: V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The Biology and Chemistry of the Compositae. Academic Press, N.Y.

TURNER, B. L., & R. M. KING. 1964. Chromosome numbers in the Compositae. VIII. Mexican and Central American species. Southwest. Nat. **9**: 27–39.

VAUGHAN, J. G. 1970. The structure and utilization of oil seeds. Chapman and Hall Ltd., London.

VRIES, M. A. DE. 1948. Over de vorming van Phytomelaan bij *Tagetes patula* L. en enige andere Composieten. H. Buurman, Leiden.

WAGENITZ, G. 1976. Systematics and phylogeny of the *Compositae (Asteraceae)*. Plant Syst. Evol. **125**: 29–46.

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CORRECT AUTHOR CITATION FOR SENECIO WERNERIAEFOLIUS

LEONARD J. UTTAL

The name *Senecio werneriaefolius* is generally cited as *S. werneriaefolius* A. Gray. It is so published by Barkley, No. Am. Flora ser II; **10:** 88. (1978) and by Greenman, Ann. Mo. Bot. Gard. **5:** 61. (1918). This is incorrect. The proper citation of this name is *Senecio werneriaefolius* (A. Gray) A. Gray. Gray first described this taxon as *Senecio aureus* var. *werneriaefolius* A. Gray, Proc. Acad. Phila. **1863:** 68. (1864). He later proposed the new combination *Senecio werneriaefolius,* A. Gray, Proc. Am. Acad. **19:** 54. (1883), based on the original varietal description with the same type: Colorado. *Hall and Harbour 331.* (GH). It is required, therefore, to cite the author as proposed above.

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A CLARIFICATION OF THE STATUS OF CAREX CRINITA AND C. GYNANDRA (CYPERACEAE)

LISA A. STANDLEY

Abstract. *Carex crinita* and *C. gynandra* are considered by some authors to be conspecific on the basis of morphological similarities. Variation in morphology, foliar anatomy, chromosomal numbers, and habitat preference among 12 populations of these taxa was studied to clarify their status and relationship. Two groups of populations are distinguished by non-overlapping qualitative differences in the morphology of perigynia, scales and sheaths. These groups appear to be reproductively isolated by differences in flowering time where they are sympatric. These taxa must be considered as distinct species on the basis of the morphological differences and reproductive isolation. Shared features of morphology, anatomy, and chromosomal number suggest that they are very closely related.

Carex is the largest and most complex genus of the Cyperaceae in temperate regions. Estimates of numbers of species range from 793 (Kükenthal, 1909) to 1500 (Airy-Shaw, 1973). Existing classifications of this taxonomically difficult group are based on the morphology of features which appear to be highly reduced and conservative. The plants are monoecious and anemophilous. A pistillate flower consists of a uniovulate gynoecium and a single style with 2 to 3 stigmas, and is included in a modified bract called a perigynium which is subtended by a single scale. The linear leaves are ligulate and have a closed tubular sheath. Variation in relatively few characters, such as the shape, size, and color of the perigynia and subtending scales, the dimensions of leaves and of involucral bracts, and differences in habit are used to distinguish species, although the extent and pattern of variation of these characters is often not understood. Various authors have used species concepts which are narrow (MacKenzie, 1935) or broad (Fernald, 1950) with regard to morphological variation. The construction of a classification of *Carex* which accurately represents the evolutionary relationships of taxa requires a more complete understanding of the patterns of variation within the genus. Morphological variation must be better understood and documented. Variations in anatomy, cytology, and reproductive biology which have been shown to be valuable in assessing relationships of taxa in the Poaceae (Stebbins & Crompton, 1961) may also be important in the Cyperaceae.

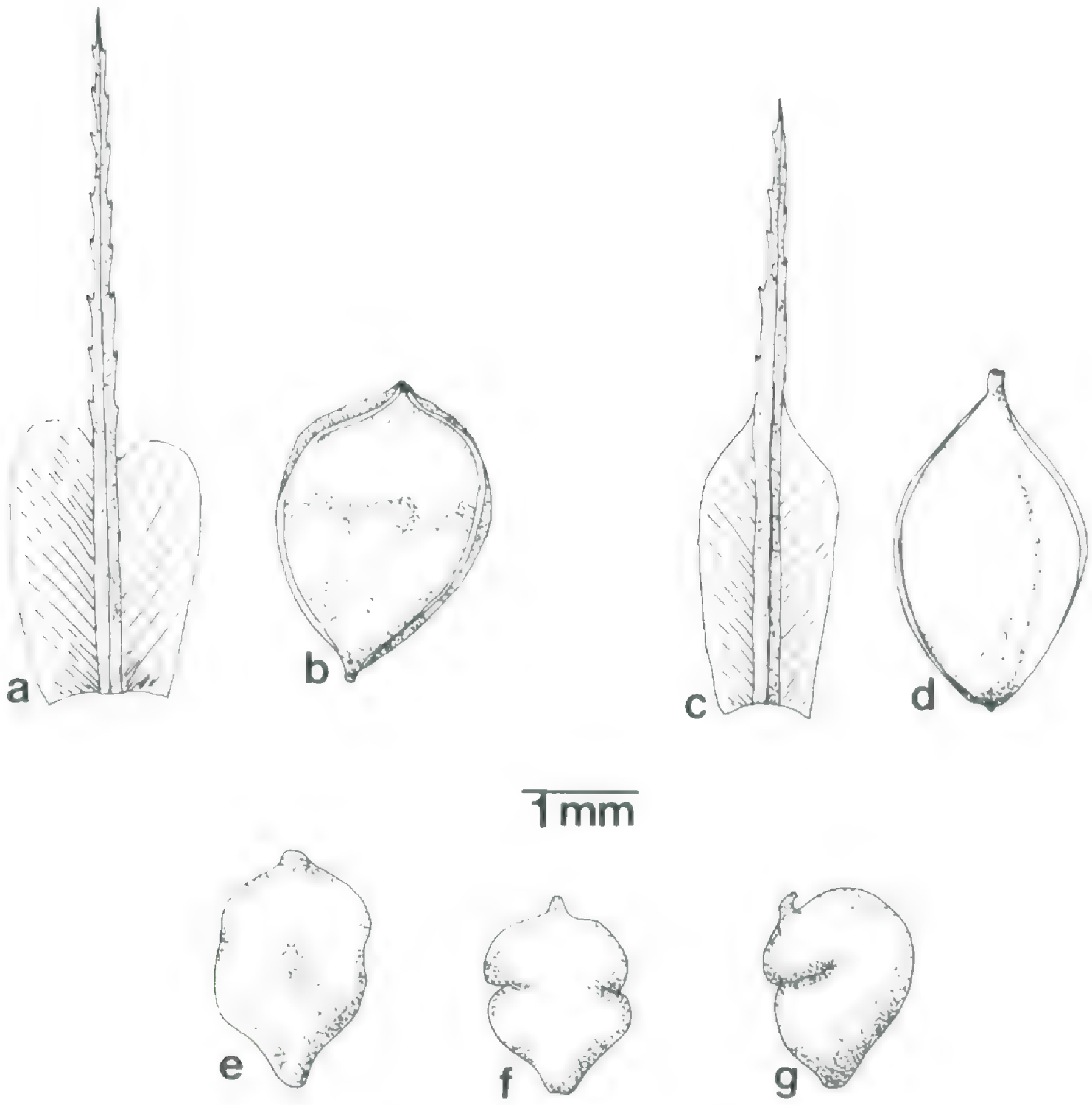

Figure 1. **Representative perigynia, achenes, and scales. A.** Pistillate scale of *C. crinita*. **B.** Perigynium of *C. crinita*. **C.** Pistillate scale of *C. gynandra*. **D.** Perigynium of *C. gynandra*. **E-G.** Achenes. (A, B, G; *C. crinita, Standley 77-95; C, D; C. gynandra, Standley 76-104:* E, F; *C. gynandra Standley 77-76*).

One specific problem which may be resolved by the application of a biosystematic analysis is the relationship of two taxa of eastern North America which are assigned to section Cryptocarpae (Fernald, 1950). *Carex crinita* Lam. and *C. gynandra* Schwein. are tall, caespitose perennials of wet sites, with pendant unisexual spikes, biconvex perigynia, awned scales, and lenticular achenes which are often invaginated on one margin. They were originally distinguished by differences in the shape of the perigynia (Schweinitz, 1824) and later by additional differences in the vestiture of the sheaths of the proximal leaves and the shape of the scales (Boott, 1858). These two taxa have been recognized as distinct species (Weatherby, 1923;

MacKenzie, 1935; Hermann, 1941) or as subspecies or varieties of a single, polymorphic species (Bailey, 1886; Fernald, 1950; Gleason & Cronquist, 1963). Complete descriptions and synonymy are provided by MacKenzie (1935). *Carex mitchelliana* M.A. Curtis of the southeastern coastal plain is morphologically similar to *C. crinita* and *C. gynandra*, but is distinguished by differences in the shape of the achenes. Although this taxon is undoubtedly part of the *Carex crinita* complex, its status will not be discussed at this time as populations have not been investigated in the field.

The present study is an attempt to resolve the problems of classification of these taxa by examining variation in morphology, foliar anatomy, chromosomal numbers, and habitats within populations in the vicinity of Ithaca, N.Y. This information, although from a limited geographic area, is useful in determining whether these two taxa should be recognized as separate species, and in clarifying their relationship.

METHODS

Eleven populations of *Carex* within a 20 km radius of Ithaca, N.Y. were sampled in this study (Table 1). Plants in each population were enumerated and a random sample of 10% of the plants in each population was chosen for study of morphological and anatomical features. For each character studied, average values are based on a single measurement per culm, with the following exceptions: the average of five measurements per culm was used for estimates of the dimensions of perigynia, scales, and achenes of each plant. To standardize measurements, only the proximal spike on a culm was chosen for study. Perigynia and their subtending scales were chosen arbitrarily from among those on the basal third of that spike.

Herbarium specimens at CU, BH, GH, NY, and TRT were examined for the construction of distribution maps and to test hypotheses developed in the study of populations. In addition, photographs of the holotype of *Carex crinita* (P, photo GH!) and the holytype of *C. gynandra* (PH!) were examined to verify the use of these names.

For anatomical study, a section 5 cm in length from the middle of the longest leaf of a randomly selected vegetative culm from each sampled plant was preserved in FAA. Transverse sections of leaves were cut with a razor blade, cleared in commercial bleach for 5 minutes, and mounted in Hoyer's solution for study.

Table 1. Descriptions of localities of populations of *Carex crinita* and *C. gynandra* studied in the vicinity of Ithaca, N.Y.

Population	Location	Elevation (m)	Habitat	Taxon
Connecticut Hill	Tompkins Co., 7.5 km W of Newfield	527	marsh	*C. gynandra
Henderson Gulf	Tompkins Co., 5 km SW of Newfield	375	marsh	*C. gynandra
Carter Creek	Tompkins Co., 0.5 km NE of Alpine	549	marsh	*C. crinita
Michigan Hollow	Tompkins Co., 5 km S of Danby	395	marsh, swamp	C. crinita
Spencer	Tioga Co., 2.5 km N of Spencer	330	marsh	C. crinita
Slaterville	Tompkins Co., 5 km N of Slaterville Springs	375	marsh	*C. crinita, C. gynandra
Six-Mile Creek	Tompkins Co., 7 km SE of Ithaca	215	marsh	C. crinita
Freeville	Tompkins Co., 0.5 km N of Freeville	318	marsh, swamp	*C. crinita, *C. gynandra
Sapsucker Woods	5 km N of Ithaca	325	marsh	*C. crinita
Lansing	Tompkins Co., 5 km W of South Lansing	335	marsh	C. crinita

*= chromosomal number determined for this population.

For study of chromosomes, collections of staminate spikes were made during the first half of May 1976. Spikes were fixed in Carnoy's solution (3:1 absolute ethanol: acetic acid, v/v) for at least 24 hours at 10° C, and stored in 70% ethanol under refrigeration. Anthers were squashed onto a slide and stained with acetocarmine according to the methods outlined by Faulkner (1972). Counts of chromosomes were obtained from metaphase plates of the first meiotic division of the microsporocytes. The majority of counts reported are based on at least five counts in each anther studied.

RESULTS

The majority of morphological characters studied exhibited little variation among populations or individuals. Dimensions of culms, leaves, bracts, spikes, scales, and achenes exhibit the same range of variation in both taxa (Table 2). These data were obtained from

Table 2. Morphology of *C. crinita* and *C. gynandra*

Character	*C. crinita* Mean	*C. crinita* Range	*C. gynandra* Mean	*C. gynandra* Range
Length of vegetative leaf	117 cm	82–165	107 cm	65–148
Width of vegetative leaf	10 mm	7– 13	10 mm	7– 13
Height of flowering culm	119 cm	73–155	116 cm	67–162
Length of involucral bract	34 cm	18– 60	26 cm	12– 46
Width of involucral bract	9 mm	6– 11	7 mm	5– 13
Length of staminate spike	6.3 cm	3.8– 9.0	4.5 cm	1.5– 6.3
Length of pistillate spike	7.2 cm	4.3–11.4	7.4 cm	5.5–10.4
Length of proximal peduncle	4.5 cm	2.0– 7.2	2.9 cm	1.5– 5.6
Length of perigynium	2.5 mm	2.0– 3.0	3.1 mm	2.4– 4.2
Width of perigynium	1.8 mm	1.5– 2.0	1.7 mm	1.5– 2.1
Thickness of perigynium	1.0 mm	.8– 1.2	1.5 mm	1.3– 1.7
Length of pistillate scale	6.0 mm	3.2–10.0	5.2 mm	3.5– 8.0
Length of awn of pistillate scale	3.9 mm	1.0– 7.5	2.8 mm	1.5– 5.8
Length of achene	1.6 mm	1.3– 2.0	1.8 mm	1.6– 2.1
Width of achene	1.3 mm	1.1– 1.4	1.3 mm	1.1– 1.4
Apex of scale	retuse		acute	
Vestiture of sheaths of proximal leaves	glabrous		scabrous	
Outline of perigynium	obovate		elliptical	

study of local populations, but are consistent with dimensions of herbarium specimens from the entire range of distribution of both taxa. Achenes are lenticular in outline but margins may be entire or invaginated along one or both margins (Fig. 1). The shape of achenes has been used to distinguish taxa within this group. I have found that the shape of the fruit commonly varies among perigynia of a single individual and is therefore not a reliable taxonomic character.

Three morphological features, vestiture of the sheaths, shape of the scales, and shape of the perigynia exhibited variation between populations (Table 2). The sheaths of leaves, particularly the sheaths of the proximal leaves, are either glabrous or scabrous. Scabrous sheaths have an average of 20 silica prickle-hairs (0.15 mm in length) per mm^2. Plants with glabrous sheaths lack prickles entirely. The scales which subtend the perigynia have a broad, 3-nerved midrib that is excurrent as an awn. The length of this awn varies within a spike, decreasing markedly toward the apex of the spike. The scale, exclusive of the awn, is obovate in outline and may be acute or retuse at the apex (Figure 1). Perigynia may be obovate or elliptical in outline (Figure 1). Obovate perigynia are rounded in their cross-sectional outline, with a characteristic width of 1.8 mm and thickness of 1.5 mm. The average length of an obovate perigynium is 2.4 mm. Elliptical perigynia are flattened in cross-sectional outline, with an average width of 1.7 mm and thickness of 1.0 mm. These have an average length of 3.0 mm. Length of the perigynia is correlated with differences in the characters of outline and cross-sectional shape, but the range of perigynium length does overlap, as shown in fig. 2, and is not a consistently reliable taxonomic character.

Patterns of variation in the character-states of sheaths, scales and perigynia are correlated. Plants with scabrous sheaths have dorsiventrally flattened, elliptical perigynia and scales which are acute at the apex. Plants with glabrous sheaths have inflated, obovate perigynia and scales which are retuse at the apex. The scatter diagram (Fig. 2) illustrates these correlations. Two groups of populations, which correspond to the two taxa, are clearly distinguishable on the basis of these three morphological features.

Leaves are shallowly plicate (Fig. 3) with an average of 40 (range, 28 46) vascular bundles separated by transversely oblong air-

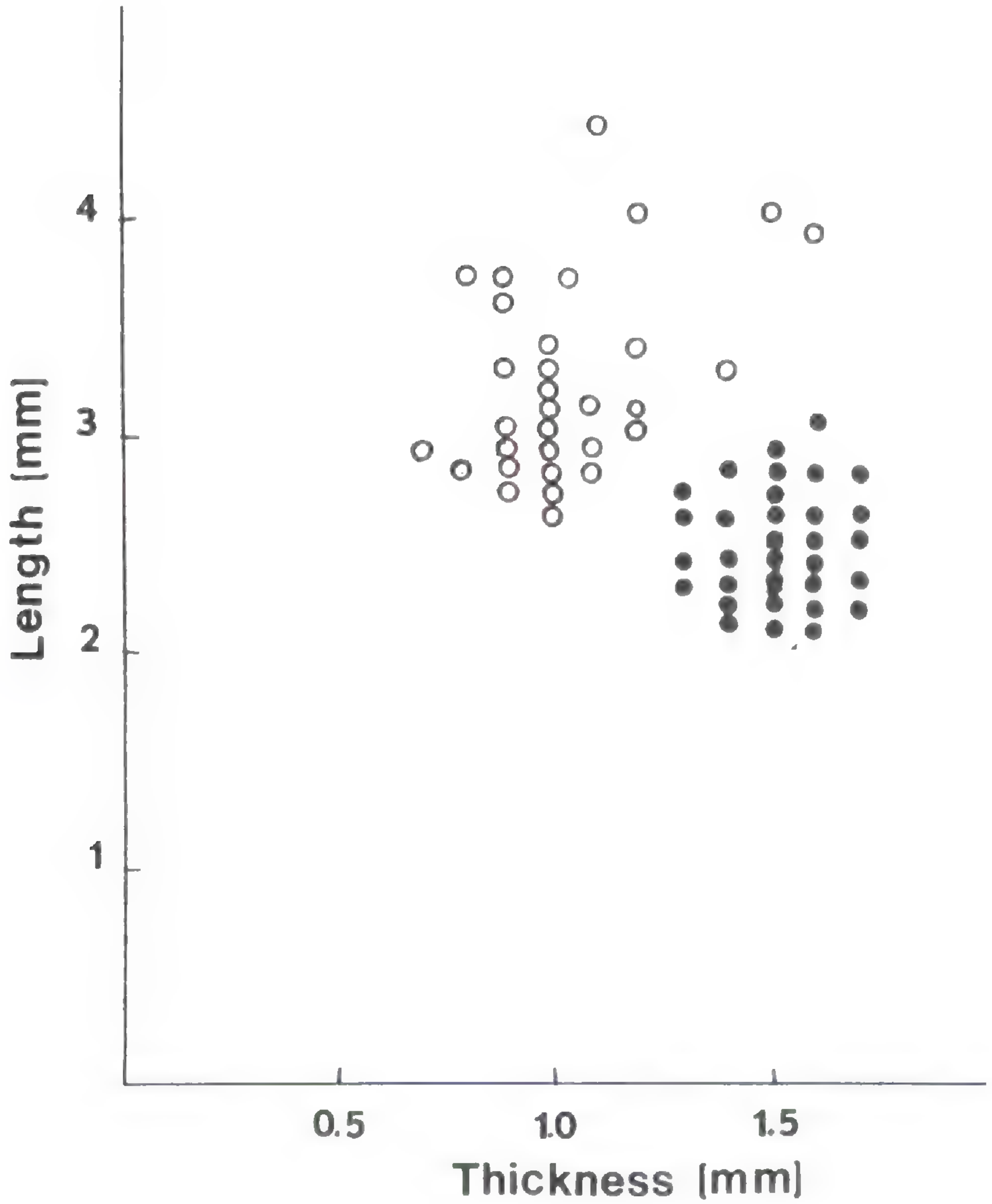

Figure 2. **Scatter diagram of dimensions of perigynia.** Open circles represent plants with scabrous sheaths (*Carex gynandra*). Closed circles represent plants with glabrous sheaths (*Carex crinita*).

cavities. The epidermal surfaces are differentiated. The adaxial epidermal surface consists of cells which lack papillae. Cells of the abaxial surface are smaller, and have a single median papilla. Stomates occur only on the abaxial surface. Bulliform cells occur in a single group adaxial to the midvein, and consist of a layer of large, thin-walled cells subtended by a layer of smaller clear cells. The adaxial projection of the midvein, or keel, may be rounded or acute

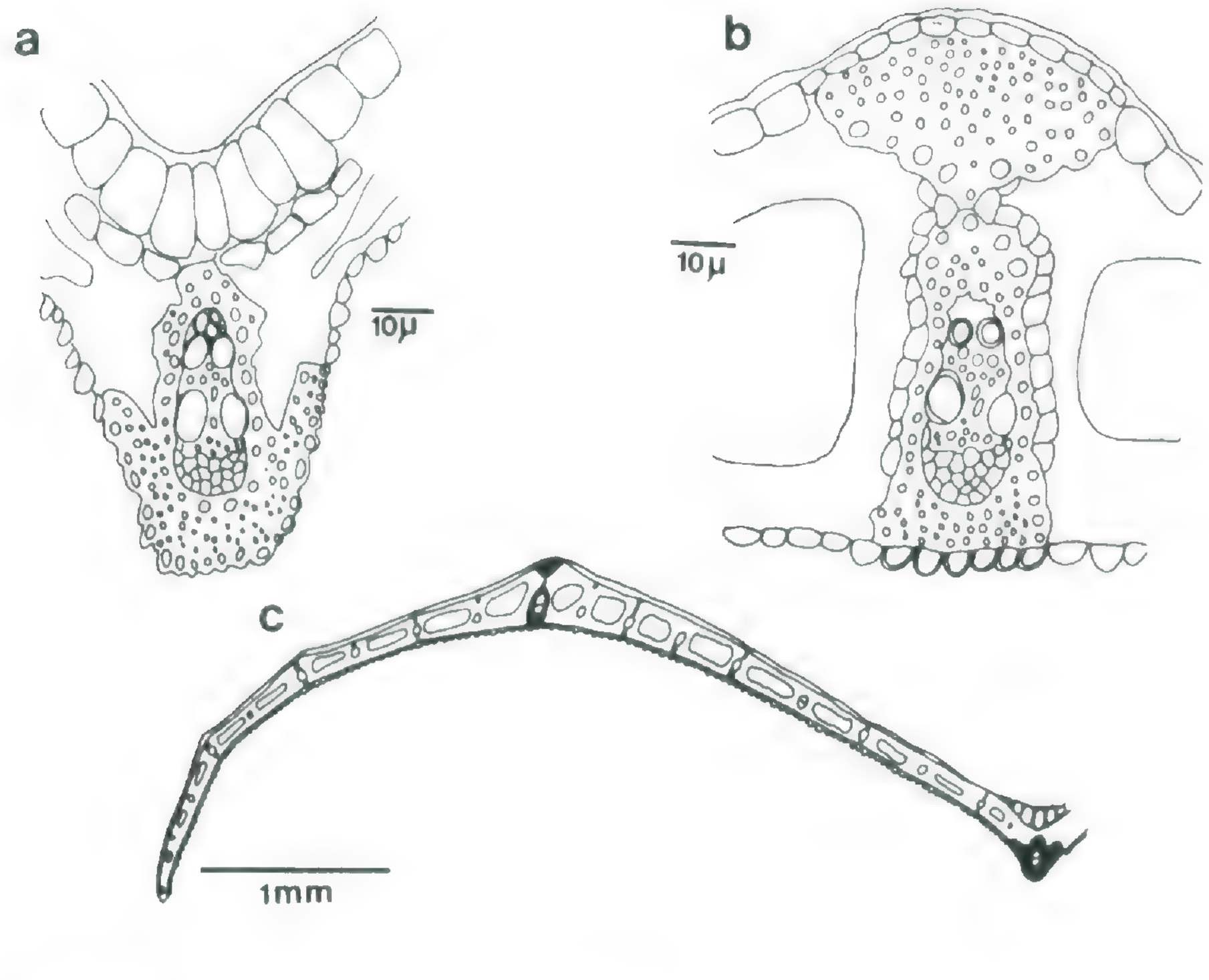

Figure 3. **Features of transverse sections of leaves of Carex gynandra** (*Standley 77 76*). **A.** Midrib, showing median vascular bundle. **B.** Secondary vascular bundle. **C.** One-half transverse section of leaf.

in transverse section. Variation in the shape of the keel was not found to be correlated with variation in other features of anatomy or of morphology. No other variations in foliar anatomy were observed.

Chromosomal numbers were obtained from five populations of plants with glabrous sheaths (Table 1). All individuals studied had 33 bivalents. No univalents or multivalents were seen, although Wahl (1940) observed both $n = 33$ and $n = 32+3$ in plants of *Carex crinita*. I examined voucher specimens for his counts at BH and GH. No morphological variation was correlated with these differences in pairing.

Populations studied in upstate New York occur in roadside ditches and in two major types of undisturbed communities with waterlogged soils. The majority of populations occurred in wet open meadows (Table 1) dominated by monocotyledons. Up to 20 species, including *Typha latifolia, Acorus calamus, Glyceria grandis, Scirpus cyperinus, Eupatorium maculatum, Impatiens capensis,* and *Onoclea sensibilis* frequently occur with *Carex* in these sites. Soils

are glacial silt-loams or gravels.

A few populations were located in wooded swamps dominated by *Acer rubrum, Alnus rugosa, Vaccinium corymbosum,* and *Viburnum dentatum*. Fewer than ten herbaceous species typically occur with *Carex* on hummocks in these swamps. These species include *Dryopteris cristata, Rubus pubescens, Symplocarpos foetidus,* and *Osmunda cinnamomea*. Soils tend to be organic mucky silts.

Although these two community types may be assumed to differ in environmental factors such as temperature, humidity, and the availability of light, differences in habitat were not correlated with morphological or anatomical differences in the populations of *Carex* which were studied.

Distribution maps of the two taxa (Figure 4) were constructed. Regional distribution maps are also provided by Braun (1967), Hermann (1941), Radford et al. (1968), Voss (1972), and Wheeler (1981). The two morphological forms have different ranges, although they are sympatric over a large part of the northeastern United States. *Carex crinita* occurs from Nova Scotia west to Wisconsin, and south to Georgia and Texas. It is uncommon in the mountains of the Appalachians and Adirondacks. Löve and Löve (1981) report a new record of this species from Winnepeg, Manitoba. *Carex gynandra* has a more limited geographic distribution. It occurs from Newfoundland west to the northern Great Lakes region, and south in the Appalachians to northern Georgia. This taxon generally occurs at higher elevations than *Carex crinita*, and is less common on the coastal plain.

The taxa are geographically sympatric over most of their range of distribution. Populations in central New York, however, generally consist of only one morphological form. Sympatric populations of both taxa occurred only in two locations within this region, the Slaterville and Freeville populations (Table 1). As the two taxa have the same chromosomal number, they would be expected to be interfertile (Faulkner, 1973; Standley, 1981) and to hybridize in the absence of other barriers to interbreeding. An examination of populations in these two localities yielded one individual which appeared to be intermediate in features of the scabrosity of sheaths, shape of the perigynia, and apical shape of the pistillate scales. No achenes developed on this plant, leading to the conclusion that it was a putative hybrid of reduced fertility.

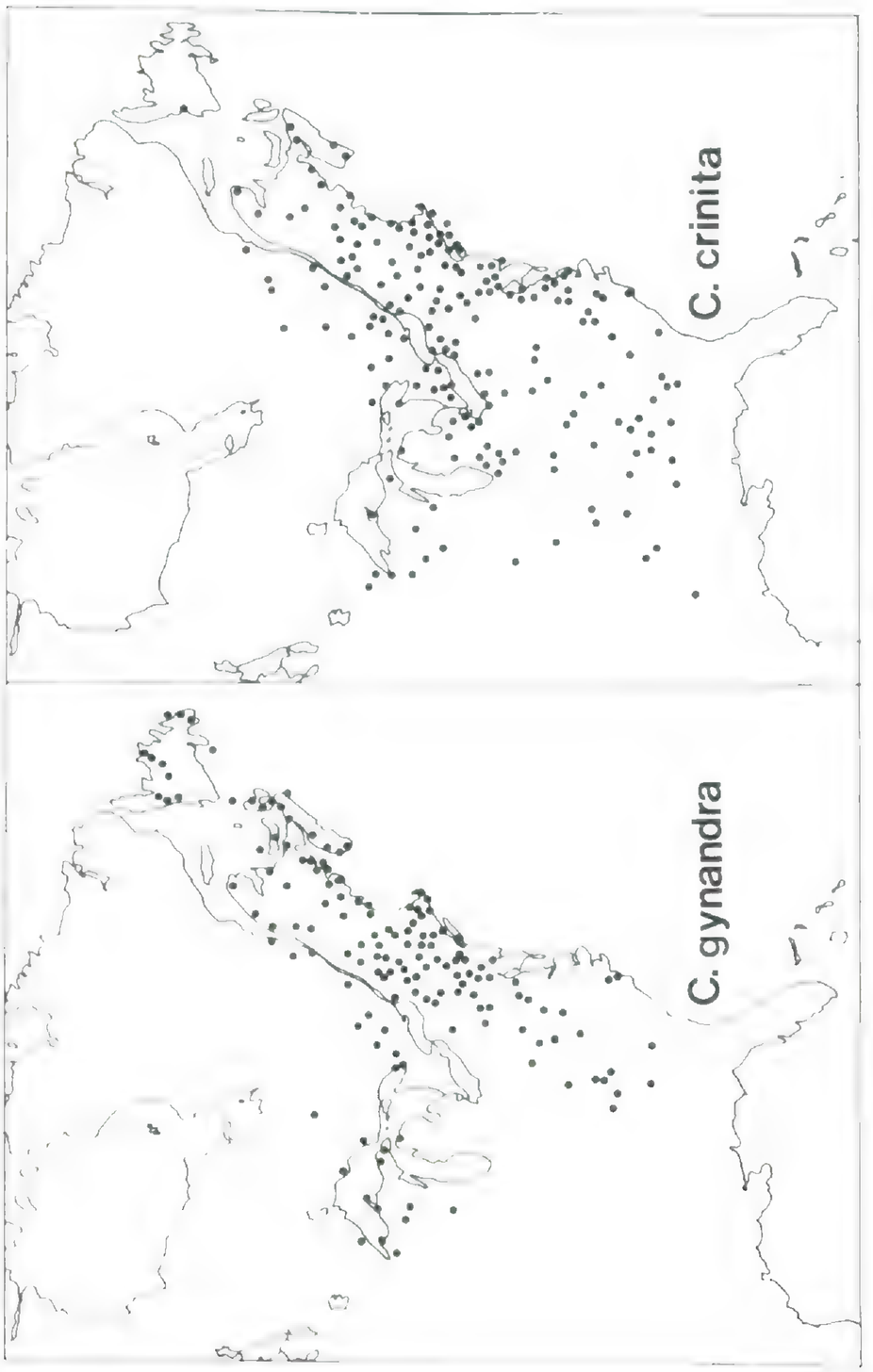

Figure 4. **Distribution maps for Carex gynandra and C. crinita.**

Differences in the phenology of flowering may act as isolating mechanisms in sympatric populations. Observations at the Slaterville site in May of 1977 indicated that plants with scabrous sheaths (*Carex gynandra*) initiated flowering at least one week later than plants with glabrous sheaths (*C. crinita*). This observation requires additional quantification, but suggests that there is little overlap of flowering time.

DISCUSSION

Carex crinita and *C. gynandra* do not differ with regard to most features of the morphology of leaves and of inflorescences, the anatomy of leaves, chromosomal numbers, and habitat preferences. Correlated variation in the morphology of perigynia, of pistillate scales, and of the sheaths of leaves is the basis for clustering populations in this study into two distinct taxa. These sets of characters differ in their geographical distribution, although taxa are sympatric over part of their range. These patterns of variation are consistent with those observed in systematic studies of related species of *Carex* (Standley, 1981) which are distinguished by morphological differences of the perigynia, scales, and inflorescences. Chromosomal numbers and foliar anatomy have been found to be most useful in clustering related species. Subspecies are defined as groups of populations which differ in their geographic distribution and which differ, although not consistently, in a few morphological characters. The two taxa distinguished in this study, *Carex crinita* and *C. gynandra*, are considered to be distinct yet closely related species in accordance with this model, as they differ consistently in morphology, overlap geographically, and appear to be reproductively isolated through differences in the phenology of flowering. Speculation on the process of divergence of these taxa requires additional evidence on the evolutionary polarity of the character-states which distinguish them. Current studies of the systematics of the Cryptocarpae and Acutae groups will attempt to resolve this question.

CONCLUSIONS

The study of populations of *Carex crinita* and *C. gynandra* in the vicinity of Ithaca, N.Y. has provided information on variation in

morphology, foliar anatomy, habitat, and chromosomal numbers. Details of foliar anatomy of both taxa and the chromosomal number of $n = 33$ for *Carex gynandra* are documented for the first time. Species are distinguished by the consistent correlated differences in the morphology of the sheaths of leaves, the perigynia, and the pistillate scales, and appear to be reproductively isolated by differences in the phenology of flowering. This study has demonstrated that problems of species classification in *Carex* can be resolved through a better understanding of the patterns of variation and reproductive interactions within the genus.

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LITERATURE CITED

AIRY-SHAW, H. K. 1973. A dictionary of the flowering plants and ferns. 8th edition. Cambridge University Press.

BAILEY, L. H. 1886. A preliminary synopsis of the genus *Carex*. Proc. Amer. Acad Sci. **22**.

BOOTT, F. 1858–1867. Illustrations of the genus *Carex*. London. Wm. Pamplin.

BRAUN, E. L. 1967. The monocotyledonae; Cattails to Orchids. Columbia, Ohio State University Press.

FAULKNER, J.S. 1973. Experimental hybridizations of northwest European species of *Carex* section *Acutae* (Cyperaceae). J. Linn. Soc., Bot. **67**: 233 253.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th edition. New York, D. Van Nostrand.

GLEASON, H. A., & A. CRONQUIST. 1963. Manual of vascular plants of the Northeastern United States and adjacent Canada. Princeton, Van Nostrand.

HERMANN, F. J. 1941. The genus *Carex* in Michigan. Amer. Midl. Nat. **25**: 1–72.

KÜKENTHAL, G. 1909. Cyperaceae: Caricoideae. Das Pflanzenreich (38 Heft) IV:20.

LÖVE, A., & D. LÖVE. 1981. *In*: A. Löve, ed. Chromosome number reports LXXIII. Taxon **30**: 845–849.

MACKENZIE, K. K. 1931–1935. Cyperaceae: Cariceae. North American Flora **18**: 1–478.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill, University of North Carolina Press.

SCHWIENITZ, L. D. VON. 1824. An analytical table to facilitate the determination of the hitherto observed North American species of the genus *Carex*. Ann. Lyceum N.Y. **1**: 62–71.

STANDLEY, L. A. 1981. The systematics of *Carex* section *Carex* in the Pacific Northwest. Ph.D. Thesis. University of Washington.

STEBBINS, G. L., & B. CROMPTON. 1961. A suggested revision of the grass genera of temperate North America. Recent Advances in Botany **1**: 133 145.

VOSS, E. G. 1972. Michigan Flora. Part 1. Gymnosperms and Monocots. Bull. Cranbr. Inst. Sci. **55**.

WAHL, H. 1940. Chromosome numbers and meiosis in *Carex*. Amer. J. Bot. **27**: 458–470.

WEATHERBY, C. A. 1923. The identity of *Carex gynandra* Schwein. Rhodora **25**: 115 116.

WHEELER, G. A. 1981. New records of *Carex* in Minnesota. Rhodora **83**: 119 124.

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NOTICE OF PUBLICATION

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CHROMOSOMES OF MEXICAN *SEDUM* IV. HETEROPLOIDY IN SEDUM MORANENSE

CHARLES H. UHL

ABSTRACT

At least 18 different chromosome numbers, from $n = 21$ to $n = 153$ are reported for 51 collections of *Sedum moranense* from 45 localities, most of them in east central Mexico. At least ten levels of ploidy, up to 16-ploid, are represented, mostly based on $x = 18$-21, including probable 5-, 7-, and 9-ploids. Dysploid variants occur at several levels of ploidy, and some other plants have extra chromosomes of standard size; at least six have B-chromosomes. In most collections the bivalents do not differ greatly among themselves in size, but four collections from the Sierra de Guanajuato have strongly asymmetrical karyotypes and also anomalous chromosome numbers ($n =$ 52, 54). In spite of the great variation in their chromosomes, most collections are very similar in their morphology, and, except for the larger flowers of the 14-ploid subspecies *grandiflorum*, no correlation is apparent between morphology and chromosome number.

This paper is the fourth in a series reporting the chromosomes of 100 or so species of Mexican *Sedum*. A general introduction, materials and methods, and acknowledgments are given in the first paper (Uhl, 1976). *Sedum moranense* is singled out for special attention here because it has the greatest cytological diversity of all the Mexican Crassulaceae, which as a group are distinguished for the great variety in their chromosomes.

The Mexican Crassulaceae have an exceptionally broad array of chromosome numbers (heteroploidy), from $n = 7$ to $n =$ ca. 320 (Uhl, 1972-1980). Polyploidy is common, ranging to at least 20-ploid, and very extensive dysploidy also occurs in some genera and in some groups of related species. In some cases a very broad range of chromosome numbers is found in plants that are very similar morphologically and that seem best regarded as all the same species. Thus construed, some species have four or more levels of polyploidy in different populations and many, perhaps most, widespread species have dysploid chromosome races (Uhl, 1972, 1978, 1980, and unpub.). For example, different populations of *Sedum wrightii* have five different levels of ploidy, $n = 12$, 24, 36, 48, and 60 (Uhl, 1972, and unpub.). On the other hand, the wide-ranging *S. jaliscanum* has at least eight different dysploid chromosome numbers, ranging from $n = 11$ to $n = 34$ (Uhl, 1976), and Clausen (1981)

would also include plants having $n = 9$ and $n = 10$ as subspecies *angustifolium* of this species. The size of the chromosomes in *S. jaliscanum* varies inversely with their number, and it seems likely that the diversity of its chromosome numbers has resulted from rearrangements of chromosome parts on a massive scale, and that polyploidy is not present.

Sedum moranense HBK is a relatively small "typical" representative of the genus (chamaephyte), with white flowers and small, ovate to lanceolate leaves that are 2 4 mm long and almost as thick as wide, closely set in five or six spiral ranks (Clausen, 1959). Clausen also reported that plants from six populations were "remarkably similar morphologically", although environmental conditions, both in nature and cultivation, can significantly affect such characters as leaf size. One other population, subspecies *grandiflorum* Clausen, had larger flowers.

Sedum moranense is one of the commonest and widest ranging species of the Crassulaceae in Mexico. It occurs as disjunct populations, most often on volcanic rock above 2,000 meters, from the southern Sierra Madre Oriental in the states of Hidalgo, Puebla, and Veracruz west to the vicinity of Mexico City and Toluca and northwest to the Sierra de Guanajuato and to the interior mountains of San Luis Potosi; it is especially common in the state of Hidalgo (Fig. 1). The species also is common in cultivation in Mexico, and the collection reported here from Jalisco may have been introduced there.

This paper presents the chromosome numbers of 51 collections of *Sedum moranense* from 45 populations in all parts of its range (Fig. 1). Collections are listed in Table 1 in order of increasing chromosome number and then approximately from west to east and from north to south. At least 18 different chromosome numbers, from $n = 21$ (Fig. 2) to $n = 153$ (Fig. 17) have been found in the species, including apparent 5-, 7-, and 9-ploids but not counting variants with one or a few extra univalents or B-chromosomes. These represent apparent diploids, polyploids of probably nine different levels, and dysploids at several levels of ploidy.

Many collections have meiotic irregularities in the form of one or more unpaired chromosomes of standard size at metaphase I and laggards at anaphase I. Most univalents are easily identified by their conspicuously shallower depth in focus than bivalents and multi-

Figure 1. Central Mexico, showing locations of plants with various gametic chromosome numbers.

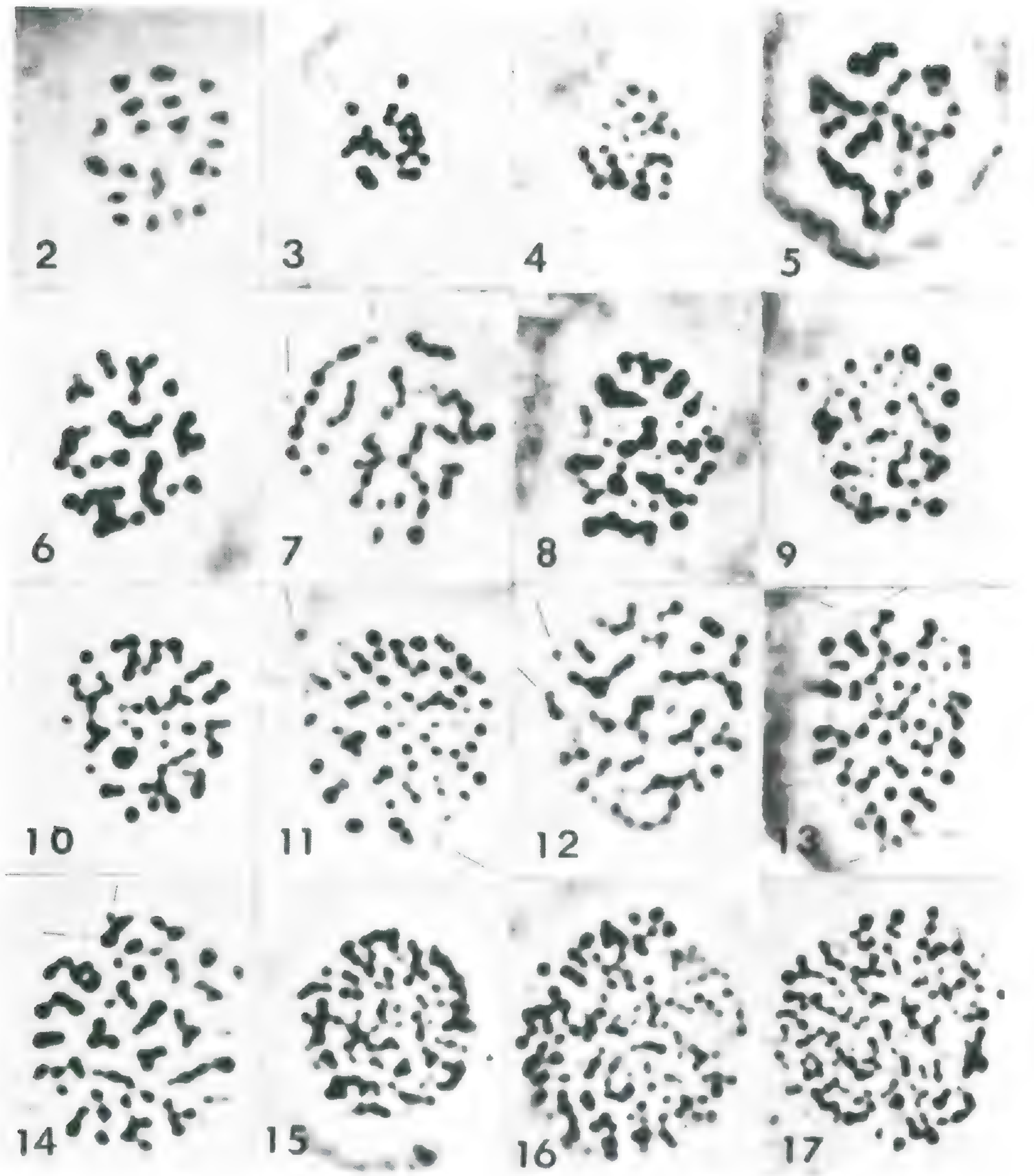

Fig. 2-17. Chromosomes of *Sedum moranense* at metaphase I, all ×2000. Thin lines in some figures indicate univalents or B-chromosomes. **2,** *U1557*, $n = 21$; **3,** *U1871*, $n = 21 + 1$; **4,** *U2353*, $n = 24$; **5,** *M13396*, $n = 38$; **6,** *M7654*, $n = 40$; **7,** *C44 109*, $n = 50 + 2B$; **8,** *M14736*, $n = 52$; **9,** *M10197*, $n = 54$; **10,** *U2069*, $n = 57$; **11,** *U830*, $n = 60 + 3$; **12,** *U2128*, $n = 62 + 2$; **13,** *8d*, $n = 63 + 6$; **14,** *M6414*, $n = 77 + 3$; **15,** *U2487*, $n = 100$; **16,** *M14734*, $n = 140$; **17,** *U1536*, $n = 153$.

valents and by their strong tendency to lie at the margins or sometimes off the plate at metaphase I. In one diploid (*U1871*, $n = 21 + 1$, Fig. 3) the unpaired chromosome is the largest present; at pachytene a heterochromatic body of about the same size is attached to the nucleolus. Very small extra, unpaired chromosomes, apparently B-chromosomes, are present in at least six collections. One diploid from Hidalgo (*U1870*, $n = 21 + 1$), two probable heptaploids from Tlaxcala (*7d* and *8d*), and one presumed octoploid from Hidalgo (*U2707*, $n = 72 \pm 1$) showed one or more chromosome bridges (up to 4) in most cells at anaphase I, presumably indicating heterozygosity for paracentric inversions.

The basic or ancestral chromosome number in *Sedum moranense* appears to be in the range of 18 to 21. Most polyploids have multiples of one or another of these numbers, up to 14-ploids with $n = 140$ in subspecies *grandiflorum* Clausen (Fig. 16) and a presumed 16-ploid (*U1536*) with $n = 153$ or very close to that (Fig. 17). Some multivalent associations are present in most cells of polyploids, and these make exact counts difficult (e.g., Fig. 10-17). Counts of plants having multivalents are reported here in terms of their equivalents as bivalents and are believed to be accurate within 2% at all levels of ploidy.

In each polyploid most cells at metaphase I generally produce a fairly constant number of bivalents, or their equivalents when multivalents are allowed for. However, especially in many of the higher polyploids, additional univalents of standard size are common at metaphase I. The number of these univalents is not constant in the cells of the same anther, which probably means that the extra chromosomes sometimes participate in forming multivalents and therefore that they are extra representatives of standard chromosomes of the genome. The species seems to be remarkably tolerant of chromosomal variation and unbalanced genetic dosages, especially at the polyploid level. Doubtless this tolerance has made possible the great variation that is found in the chromosomes of different populations.

One collection from Hidalgo (*U2343*) regularly had 40 paired elements (bivalents and multivalents) but also had 5-11 univalents of standard size and may represent a pentaploid based on $x = 20$. Two plants from the same population in Tlaxcala (*7d* and *8d*) had 60-62 paired elements plus 5-9 univalents (Fig. 13), and a plant from just

Table 1. Collections Studied.

$n = 21$	*U2129* Qro. 1 km. W. of San Joaquin, 2360 m.
	U1870 Hgo. E. of Cuesta Colorada, 13 km. N. of Jacala, 1700 m. ($n = 21 + 1$)
	U1871 Hgo. 1 km. N. of Minas Viejas, 2000 m. ($n = 21 + 1$)
	U1950 Hgo. 1 km. S. of Minas Viejas, 2040 m.
	U1557 Hgo. 11 km. E. of Tulancingo
$n = 24$	*U2353* Pue. 10 km. SW of Aquixtla, 2750 m.
$n = 38$	*U2708* Hgo. Ca. 1 km. N. of El Salto, km. 253 *(R.T. Clausen CMP-ES)*
	M13396 Hgo. Near summit of mountain SE of Santuario, 2560 m. (R. Moran and C.H. Uhl)
	C47-43 Hgo. Ca. 20 km. E. of Pachuca, 2320 m. (E.J. Alexander, via R.T. Clausen)
	C47-38 Tlax. Barranca near San Bernabe Amaxac de Guererro (Ibid.)
$n = 40$	*M7654* SLP. Zaragoza (R. Moran)
	U2705 SLP. 5 km. NW of La Salitrera *(R.T. Clausen 77-40)*
	M7809 Hgo. San Vicente, ca. 3 km. S. of Durango (R. Moran) ($n = 40 + 3B$)
	M7781 Hgo. Pachuca (R. Moran) ($n = 40 + 1 + 5B$)
	U618, UC44-110 Cultivated
Probable pentaploid	*U2343* Hgo. 4.3 km. S. of Durango, 2130 m. ($n = 40 + 5$–11)
$n = 50$	*FL1419* Cultivated ($n = 50 + 1B$)
	C44-109 Cultivated ($n = 50 + 2B$)
$n = 52$	*M14736* Gto. Santa Rosa, 2590 m. (R. Moran)
	U2288 Gto. 3 km. SW of Mesa San Jose and 22 km. NE of Guanajuato, 2360 m.
$n = 54$	*U2267* Gto. 10 km. NE of Guanajuato, 2560 m.
	M10197 Gto. Near Santa Rosa (R. Moran) ($n = 54 + 1B$)
$n = 57$	*U2069* Jal. SW edge of Tapalpa, 2130 m. (F. C. Boutin & M. Kimnach)
	U1952 Qro. 5 km. S. of Pinal de Amoles, 2560 m.
	U1854 Qro. 8.5 km. S. of Pinal de Amoles, 2600 m.
	U1476 Hgo. Presa Madero, 12 km. W. of Huichapan
	U1484, *U1485* Edo. Mex. 10.5 km. WNW of Soyaniquilpan (N.W. Uhl & W. Handlos)
	U1481 Hgo. 7.5 km. SE. of Tepeji del Rio (N.W. Uhl & W. Handlos)
	U1877 Hgo. 2 km. S. of Tepenene
	U1466 Hgo. Near Pueblo Nuevo
	C47-44 Pue. Near Honey. (H. Xolocotzi, via E. J. Alexander & R. T. Clausen)
	U1554 Pue. 22 km. NW of Zacatlan
	U1418 Edo. Mex. Hill N. of Toluca, 2740 m.
	6d Ver. Near Las Vigas (R. T. Clausen) ($n = 57 + 3$)
	U1884 Ver. 27 km. NW of Jalapa, 2290 m.

$n = 60$	*U830* Hgo. El Chico, 3000 m. (H. E. Moore) ($n = 60 + 2$)
$n = 63$	*U2128* Qro. 13 km. W. of San Joaquin, 2330 m. ($n = 63 + 1$) *U1556* Pue. Puente Totolapa, 11 km. W. of Huauchinango *U2706* Edo. Mex. El Zarco, Sierra de las Cruces (R. T. Clausen 55-169)
Probable heptaploids.	*7d, 8d* Tlax. Atlihuitzia (R. T. Clausen) ($n = 60$–$62 + 5$-9)
$n = 72$	*U2707* Hgo. Cerro Jardin, W. slope, 2480 m. (R. T. Clausen 76–47)
$n = 77$	*M6414* Hgo. Canon Venados (R. Moran) ($n = 77 + 3$)
Probable 9-ploid	*U1548* Hgo. 2 km. S. of Epazoyucan ($n = 80 + 10$)
$n = 100$	*U2487* Pue. 1 km. W. of Nicolas Bravo, 2600 m. (one clump only)
$n = 140$	*10d* SLP. Mountains (Sierra de Alvarez) E. of San Luis Potosi (R. T. Clausen) Clonotype of *S. moranense* ssp. *grandiflorum*) *U1641* SLP. 2 km. W. of highway summit, Sierra de Alvarez, 2260 m. (W. Handlos) *M14734* Gto. Picachos de la Bufa, cliffs NE of Guanajuato, 2290 m. (R. Moran)
$n = 153$	*U1536* SLP. 16 km. N. of Ahualulco

west of Mexico City (*U2706*) formed about 57 paired elements and 5-8 univalents; these three are believed to be heptaploids based on $x = 19$-21. Another plant from Hidalgo (*U1548*) had probably 80 paired elements plus about 10 univalents and is thought to be 9-ploid. Presumably the number of chromosomes of the last (odd) set that participate in the formation of multivalents is variable, which leaves a variable number of them as univalents in different cells.

In most plants the bivalent chromosomes at metaphase I do not differ greatly among themselves in size (Fig. 2, 5, 6, etc.), and any extra univalents that may be present also appear to be of the same size. However, four collections from the Sierra de Guanajuato differed strikingly from nearly all other collections in having a wide range of sizes among their 52-54 bivalents at metaphase I (Fig. 8, 9). This condition (heterogeneous or asymmetrical karyotype) is generally believed to have been derived by unequal translocations from ancestors having chromosomes more nearly equal in size (homogeneous or symmetrical karyotype) (Stebbins, 1971). The numerically anomalous diploid from Puebla (*U2353*, $n = 24$) also has bivalents that differ more than usual in size (Fig. 4), although not as much as they do in the plants from Guanajuato. Two collections with $n = 50$, both of unknown provenance from the wild, have

bivalents that are more or less equal in size, although their 1 or 2 extra chromosomes are tiny and interpreted as B-chromosomes (Fig. 7).

With so many chromosome races and so many levels of ploidy, some of them occurring close to each other, it is probable that considerable intercrossing has occurred between plants having different chromosome numbers and that such intercrossing has been a source of still more cytological variation. The evident viability and tolerance of unbalanced chromosome dosages would make survival possible until new, more or less stable chromosome complements evolved. However, the phenotypic effects of this sort of variation, including some apparent cases of unbalanced dosages of chromosomes, appear to be negligible. The effects, if any, on fertility or adaptation to the particular habitat are not clear. It is possible that some apomixis occurs here, but as yet there is no direct evidence for it. Qualitative and quantitative chemotaxonomic studies on these plants might prove interesting.

According to Clausen (1959) *Sedum liebmannianum* of the Sierra Madre del Sur is the species most closely related to *S. moranense*, but it differs conspicuously in its persistent, withered leaf bases. Two collections of *S. liebmannianum* had $n = 34$, but seven other collections were very irregular at meiosis and probably odd-ploid. A similar plant from Puebla with smaller leaves (*U2358*) had $n = 30$. Clausen (1959) also cited two other species as related to *S. moranense*: *S. cupressoides* ($n = 29$) of the Sierra Madre del Sur and *S. parvum* ($n = 32, 34, 64$) of northeastern Mexico, to which he later (1978) also reduced *S. nanifolium* ($n = 26, 52$). Chromosome numbers of these species (all from Uhl, unpublished) do not support any conclusion that they are closely related to *S. moranense*.

Clausen (1959) studied a plant said to have come from high on the Nevado de Toluca that he thought might be a hybrid between *Sedum moranense* and *Villadia batesii*. The plant is intermediate in morphology and produces abortive pollen and ovules. Eight cells at metaphase I had 24 to 27 bivalents and multivalents plus 3 to 14 univalents, and the microspores after meiosis differ among themselves in size and stainability. Nineteen collections of *V. batesii* from Puebla and Hidalgo to Michoacan, including one from the Nevado de Toluca, all had $n = 25$, which is considered to represent a diploid here (Uhl, unpublished). However, no collection of *S. moranense*

from the Nevado de Toluca has been studied, and Clausen (1959) does not cite this as a locality for the species. The nearest *S. moranense* that has been studied came from just north of the city of Toluca, about 24 km. north of the volcano, and had $n = 57$, considered hexaploid. Clausen's plant appears clearly to be a hybrid, but its chromosomes and its location make it very doubtful that *S. moranense* could have been one of its parents.

Clausen (1981) suggested that *Sedum furfuraceum* ($n = 34$, Uhl, 1980), which is known from only one population in San Luis Potosi, might have originated at that site as a hybrid between *Pachyphytum hookeri* and *S. moranense*, both of which occur with it there. However, *S. moranense* there (*M7654*) is tetraploid ($n = 40$), and *P. hookeri* there is decaploid (n = ca. 160, Uhl and Moran, 1973), and this suggested relationship seems most unlikely.

Many hundreds of hybrids have been produced in cultivation within and between *Sedum* and various other Mexican genera. However, only one cross has been attempted with *S. moranense; U1642* (*S. retusum*, $n = 27$, Uhl, 1980) × *U1557* (S. moranense, $n = 21$), and this was unsuccessful. Analysis of chromosome pairing in hybrids of *S. moranense* having different chromosome numbers could allow their levels of ploidy to be identified, as has been done with *Echeveria* (Uhl, 1982ab).

LITERATURE CITED

Clausen, R. T. 1959. *Sedum* of the Trans-Mexican Volcanic Belt. Cornell Univ. Press, Ithaca, NY.

_____. 1978. *Sedum*—seven Mexican perennial species. Bull. Torrey Bot. Club **105:** 214–223.

_____. 1981. Variation of Species of *Sedum* of the Mexican Cordilleran Plateau. Ithaca, NY.

Stebbins, G. L. 1971. Chromosomal Evolution in Higher Plants. Edward Arnold, London.

Uhl, C. H. 1972. Intraspecific variation in chromosomes of *Sedum* in the southwestern United States. Rhodora **74:** 301–320.

_____. 1976. Chromosomes of Mexican *Sedum* I. Annual and biennial species. Rhodora **78:** 629–640.

_____. 1978. Chromosomes of Mexican *Sedum* II. Section Pachysedum. Rhodora **80:** 491–512.

_____. 1980. Chromosomes of Mexican *Sedum* III. Sections Centripetalia, Fruticisedum and other woody species. Rhodora **82:** 377–402.

_____. 1982a. The problem of ploidy in *Echeveria* (Crassulaceae) I. Diploidy in *E. ciliata*. Amer. J. Bot. **69:** 843–854.

———. 1982b. The problem of ploidy in *Echeveria* (Crassulaceae) II. Tetraploidy in *E. secunda*. Amer. J. Bot. **69:** 1497–1511.

——— & Reid Moran. 1973. Chromosomes of *Pachyphytum* (Crassulaceae). Amer. J. Bot. **60:** 648–656.

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PATCHES, CLONES AND SELF-FERTILITY OF MAYAPPLES (*PODOPHYLLUM PELTATUM* L.)

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ABSTRACT

Mayapples (*Podophyllum peltatum* L.) grow in patches on the forest floor. Controlled pollinations within and between patches, as well as self-pollinations, indicate that the mayapple is self-sterile in only part of its range, and that in this part of the range, the patches are not single clones, i.e. they consist of more than one genotype.

The mayapple, *Podophyllum peltatum* L., is a common rhizomatous, perennial herb in deciduous forests of eastern North America. It grows in well-defined patches over much of its range, and the form of these patches suggests a clonal development. The patches have been called clones by Rust and Roth (1981), Taylor (1974), and Krochmal, et al. (1974), but those authors did not attempt to investigate the population structure of the patches. Since there is considerable theoretical interest in the structure of populations of asexually reproducing herbs (e.g. Williams, 1975), I wanted to know whether mayapple patches are in general composed of only one genotype, or whether there is more than one genotype per patch.

Mayapples proliferate shoots asexually (Sohn & Policansky, 1977; Holm, 1899), and thus there are fewer genotypes than shoots in a mayapple patch. Given self-sterility, one would expect fewer fertile crosses within patches than between them, because some crosses would be between members of the same genotype. If the patches were single clones then all intra-patch crosses would be sterile. In this paper I report the results of such experimental crosses.

METHODS

I studied mayapples in Bowers Woods, north of Valparaiso, Indiana, in 1976; in the Institute for Advanced Studies, in Princeton, New Jersey, in 1976; in Oak Ridge, Tennessee, in 1975 and 1976; and at the Case Estates of the Arnold Arboretum, Weston, Massachusetts, in 1975 and 1981. At the Case Estates there is one very

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large, poorly-defined patch of probably introduced mayapples. This patch is bisected by a footpath. At the other sites there are numerous well-defined patches of various sizes.

Flower buds were covered with numbered, brown paper bags. At anthesis, pollinations were made between shoots within and between patches, as well as self pollinations. Following the pollinations the bags were replaced. Some flowers were left bagged with no treatment throughout the experiments; others were destaminated, and left bagged. Later in the summer the fruits were examined. At the Case Estates in Massachusetts in 1981 I counted the seeds in each fruit; in the other sites only presence or absence of seeds and fruit size were recorded. There is a good correlation between seed number and fruit size (Sohn & Policansky, 1977).

RESULTS

Some of the experiments in Oak Ridge, and those in Bowers Woods did not yield clear results. Some of the selfed plants produced a few seeds, but most of them and many of the outcrossed plants did not. It appears that self-sterility is not complete at those sites. Clear results were obtained in one Oak Ridge site, in Weston, and Princeton; they are presented for comparison in Table 1.

There was some degree of self-fertility in the populations in Weston and Oak Ridge (Table 1). Additionally, in Weston in 1981, of 12 selfed flowers, 2 produced 1 seed each, and 1 produced 18 seeds. Four outcrossed flowers produced 0, 2, 46, and 53 seeds. Of 99 unbagged flowers, 63 failed to set seed, and of the 36 that did, the number of seeds ranged from 1 to 70, with a mean of 26.3.

Table 1. Proportion of experimental pollinations resulting in production of at least one seed.

LOCALITY AND DATE	SELFED	CROSSED WITHIN PATCH	CROSSED BETWEEN PATCHES
Oak Ridge, 1975	4/6	7/10	—
Weston, 1975	3/23	8/10	—
Weston, 1981	3/12	3/4	—
Princeton, 1975	0/46	8/27	12/12

In Princeton three clearly defined patches showed complete self-sterility. Of 13, 15, and 18 flowers selfed in the three patches none set any seeds, while 2 out of 6, 1 out of 11 and 5 out of 10 flowers outcrossed within the patches set seeds. The difference in proportion of flowers setting seed between selfed and outcrossed flowers is significant by chi-square test at the .01 level. Four flowers from each patch were cross-pollinated with 4 flowers from adjacent paches; all of these set seed.

None of the destaminated flowers or those that were bagged without pollination set any seeds at any of the sites. The proportion of flowers setting seed in untreated populations ranged from zero in a central Tennessee population in 1975 to around 80% in Princeton in 1975 and 1976.

DISCUSSION

The analysis of patches in Princeton demonstrates that they are not single clones. Although self-pollinations never resulted in seeds, pollinations within patches sometimes did, and pollinations between patches always did (Table 1). It is impossible to say how many genotypes there were in each of the three patches. There may have been only two, but there were definitely more than one.

There appears to be considerable variability in the degree of self-fertility over the range of mayapples. The results of this study indicate that the mayapple is not completely self-sterile over all of its range, but that it is in Princeton. Recently Swanson and Sohmer (1976) made some inter- and intrapopulation crosses of mayapples in Wisconsin, to test the hypothesis that interpopulation crosses would be more fertile than intrapopulation crosses. This hypothesis was confirmed. They did not report the results of any self-pollinations, but the low fertility of their intrapopulation crosses in Wisconsin suggests that the plants are probably self-sterile there also.

Williams (1975) presented a model for the evolution of sex in asexually reproducing plants, such as the strawberry. He assumed that single clones formed patches of shoots that were better adapted to their own local environment, due to natural selection, than other clones in the general area. Mayapples grow very much like strawberries, and thus Williams' model applies to them also. The demonstration that at least some of the patches have more than one genotype means that one of the assumptions of the model may not be generally applicable.

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LITERATURE CITED

HOLM, T. 1899. *Podophyllum peltatum*, a morphological study. Bot. Gaz. Chicago **27**: 419–433.

KROCHMAL, A., L. WILKINS, D. VAN LEAR, & M. CHIEN. 1974. Mayapple. U.S. Forest Serv. Res. Pap. **NE-296**. 9 pp.

RUST, R. W., & R. R. ROTH. 1981. Seed production and seedling establishment in the mayapple, *Podophyllum peltatum* L. Amer. Midl. Nat. **105**: 51–60.

SOHN, J. J., & D. POLICANSKY. 1977. The costs of reproduction in the mayapple *Podophyllum peltatum* (Berberidaceae). Ecology **58**: 1366–1374.

SWANSON, S., & S. H. SOHMER. 1976. Reproductive biology of *Podophyllum peltatum* (Berberidaceae): the comparative fertility of inter- and intrapopulational crosses. Wisc. Acad. Sci., Arts & Lett. **64**: 109–114.

TAYLOR, F. G. 1974. Phenodynamics of production in a mesic deciduous forest, p. 237–254 *In:* H. Lieth (ed.) Phenology and seasonality modeling. Springer, NY.

WILLIAMS, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, NJ.

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CHROMOSOMAL TYPIFICATION OF SISYRINCHIUM BERMUDIANA L. (IRIDACEAE)[1]

L. MICHAEL HILL

Literature reports for the chromosome number of *Sisyrinchium bermudiana* L. are $2n = 96$ (Oliver & Lewis, 1962), $2n = 82$, 84, 88 and 90 (Ingram, 1967), $2n = 80$ and 96 (Ingram, 1968) and $2n = 32$, 64 and 96 (Mosquin, 1970). Geographical data from voucher specimens which produced these numbers are from North America and Europe. While variation in chromosome number of a plant species is not uncommon, these data are perplexing in the light of the statements by Hemsley (1884), Bicknell (1896), and Britton (1918) that the name *S. bermudiana* L. should be applied only to the Bermudas. The latter author believed the species to be endemic to those islands. Ward's (1968) thorough nomenclatural study revealed that *S. bermudiana* L. is applied only to the Bermuda population and then listed five names of northeastern North American species (*S. angustifolium* Mill, *S. mucronatum* Michx., *S. arenicola* Bickn., *S. montanum* Greene, and *S. atlanticum* Bickn.) which were morphologically differentiated from each other, as well as *S. bermudiana* L.

It therefore becomes necessary to determine the chromosome number of *Sisyrinchium bermudiana* L. in its probable singular location: Bermuda. Flower buds from several populations were sampled and cytologically examined using an aceto-orcein technique described elsewhere (Hill & Rogers, 1970). The preparations were studied under oil at 1000× magnification using a Zeiss phase contrast microscope. Camera lucida drawings have been attached to the herbarium sheets of voucher specimens deposited in the herbarium of Bridgewater College (BDWR). The chromosome number of all populations was $n = 32$.

Sisyrinchium bermudiana in Bermuda easily shows morphological differentiation from the eastern North American species discussed by Ward (1968). The taxon has these distinguishing characteristics: a large flower (17–20 mm in diameter), a stout stem with wings 2–3 mm wide, leaves 5–7 mm wide and as stout as the stem,

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[1]This paper represents contribution number 894 from the Bermuda Biological Station for Research, Ferry Reach 1–15 West, Bermuda.

and a prominent node which is at the base of both foliaceous and spathodal bracts. A re-examination of the vouchers cited by Oliver and Lewis (1962) and Mosquin (1970) is now in progress as part of a continuing study of chromosome numbers of eastern North American taxa of *Sisyrinchium*.

This study was supported by NSF grant DEB 8008808 through the Bermuda Biological Station for Research and NSF grant TFI-8016238.

LITERATURE CITED

Bicknell, E. P. 1896. The Blue-eyed grasses of the eastern United States (genus *Sisyrinchium*). Bull. Torrey Bot. Club **23:** 130–137.

Britton, N. L. 1918. Flora of Bermuda. Hafner Press, New York.

Hemsley, W. B. 1884. *Sisyrinchium bermudiana*. J. Bot. **22:** 108–110.

Hill, L. Michael, & O. M. Rogers. 1970. Chromosome numbers of *Aster blakei* and *A. nemoralis*. Rhodora **72:** 437–438.

Ingram, R. 1967. On the identity of Irish populations of *Sisyrinchium*. Watsonia **6:** 283–289.

———. 1968. Breeding barriers in some species of *Sisyrinchium*. New Phytol. **67:** 197–204.

Mosquin, T. 1970. Chromosome numbers and a proposal for classification in *Sisyrinchium* (Iridaceae). Madroño **20:** 269–275.

Oliver, Royce L., & Walter H. Lewis. 1962. Chromosome numbers of *Sisyrinchium* (Iridaceae) in Eastern North America. Sida **1**(1): 42–48.

Ward, D. B. 1968. The nomenclature of *Sisyrinchium bermudiana* and related North American Species. Taxon **17:** 270–276.

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THE TYPE LOCALITY OF *SEDUM PUSILLUM* MICHX. AND *SENECIO TOMENTOSUS* MICHX.

LEONARD J. UTTAL

The type locality of *Sedum pusillum* Michx. is cited in Michaux (1803) as "HAB. in Carolina septentrionali, loco dicto *Flat-rock.*", that of *Senecio tomentosus* Michx. as "HAB. in Carolinae loco dicto *Flat.-Roc.*". In the gazetteer of the introduction to the facsimile edition of the Michaux flora, Ewan (1974) identifies "Flat-rock" as near Hendersonville, Henderson County, North Carolina. This Flat Rock is a well-known resort village of the North Carolina mountains but it is really not the type locality of these two species. Neither occurs in the Appalachian highlands. *Sedum pusillum* is an endemic of piedmont granite outcrops of South Carolina with one station in adjacent North Carolina. *Senecio tomentosus,* while mainly a species of the southeast United States coastal plain, also occurs on piedmont rocks in South Carolina and Georgia. The true type locality of these species is another Flat Rock, in northern Kershaw County, South Carolina, not a community but a huge granite outcrop, now a quarry producing a beautiful monument stone highly esteemed in the industry. It is crossed by State Road 58, "Flat Rock Road", 8.3 miles south of Heath Springs, Lancaster County, South Carolina (one-half mile south of the north Kershaw County boundary). It is marked on the Kershaw County road map and on the Camden quadrangle topographic map. Highway 58 is the original main road between Camden and Lancaster, frequently travelled in colonial and early republican days, known then as "The Catawba Path". Flat Rock and its neighboring crag to the north, Hanging Rock, were landmarks on this road. Michaux trvelled this road often en route between his headquarters in Charleston and regions in the mountains and further. Early geography of this region of South Carolina was gleaned from Hooker (1953), while Michaux's routes were extracted from his journals as published by Sargent (1889).

There is no evidence in his journals that Michaux ever passed through Flat Rock, North Carolina, but there are two entries which indicate he passed the Flat Rock of South Carolina. On 23 April 1795, he passed "par Flat rock, par Hanging rock Creek et couché à

Cane Creek, Lancaster County. . . ". He passed early in the day, and there are no botanical notes for this date. On 6 April 1796, en route from Illinois to Charleston, Michaux passed the night near Hanging Rock and on 7 April he proceeded to Camden, collecting a little along the way. On this route he would have to pass Flat Rock. I believe he obtained the specimens of *Sedum pusillum* and *Senecio tomentosus* on this leg of his journey. The label of the specimen of *Sedum pusillum* flatly states "Flat rock" in Michaux's hand. The plants are in prime anthesis, as they would be on 7 April. The label of *Senecio tomentosus* says "Sur un Rocher, Flat roc or hanging roc". The languages are mixed. The specimen is mostly in bud; only a few of the lower heads have expanded rays. It is in a state of pre-anthesis as would be expected on that date. Thus it is believed that 7 April 1796 is the date of collection of both type specimens. Both are in P and were seen as photographs in the IDC Microfiche set 6211.

It is generally accepted that Michaux, while given full credit for the Flora boreali-americana, did not write it. L. C. M. Richard is generally believed to be the anonymous author (Stafleu and Cowan, 1981). The variation in stated habitat between written label and printed citation in this case is not the only one in the Michaux flora.

Kershaw, the type locality county of *Senecio tomentosus*, is not dotted on the map for this species in Radford, Ahles, and Bell (1968). A dot should also be placed on the map for Pickens County as the species was collected from Table Rock by Buckley in 1843–44 (GH). These are two resumed counties of record for South Carolina for this species, recently overlooked.

On 19 and 20 April 1982 I visited the Flat Rock of South Carolina and two other granite bosses of that state long popular with field botanists. I did not find either type species discussed in this paper at Flat Rock. The extensive quarrying seems to have eradicated them as well as most of the other vegetation. I doubt if topotypes will ever be found. Outside the quarried area I did collect a specimen of *Senecio anonymus* Wood heavily suffused with the lanate tomentum usually associated with *S. tomentosus*. It might be a persistant introgressant, suggesting *S. tomentosus* had been here. Hybridization between these species occasionally occurs on the granites of South Carolina and Georgia.

The other bosses visited were 40-Acre Rock, in Lancaster County, and the huge one at the base of Caesar's Head, in Greenville County. The endemic flora and other plants of the vernal pools and mossy pockets of these bosses are seriously endangered by heavy human pressure. The habitat is very fragile. I suppose this is true of other large outcrops I was not able to visit. It is hoped efforts will be made to preserve some of these unique areas and their threatened floral elements.

ACKNOWLEDGMENTS

The author wishes to thank the foreman of the Flat Rock Quarry for permission to explore the property, for useful local geographical information and for his personal botanical observations. The curators of GH and MO are thanked for the loan of specimens used in this study. Financial assistance was received gratefully from the Virginia Flora Committee.

LITERATURE CITED

EWAN, J. 1974. Introduction to facsimile edition of Flora boreali-americana by A. Michaux.

HOOKER, R. J., ed. 1953. The Carolina backcountry on the eve of the revolution. Chapel Hill.

MICHAUX, A. 1803. Flora boreali-americana. Paris and Strasbourg.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. 1968. Manual of the vasular flora of the Carolinas. Chapel Hill.

SARGENT, C. S. 1889. Portions of the journal of André Michaux. Proc. Am. Phil. Soc. **26:** 1 145.

STAFLEU, F. A. $ R. S. COWAN. 1981. Taxonomic Literature. **III:** Lh-O. The Hague.

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PHYSOSTEGIA VIRGINIANA VAR. ARENARIA SHIMEK, AN OVERLOOKED NAME

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In a recent monograph of the genus *Physostegia* (Cantino, 1982), an obscure but validly published name was overlooked. *Physostegia virginiana* (L.) Benth. var. *arenaria* Shimek, Bull. Lab. Nat. Hist. Iowa State Univ. **6** (2): 223 (1911), was described as a new variety in a footnote to an ecological treatise on Iowa prairies. There appears to have been only one mention of the name in print since its initial publication (Guldner, 1960). Even Shimek never again used it, either in print or on herbarium labels.

From the description, Shimek's variety is clearly referable to *Physostegia virginiana* (L.) Benth. ssp. *praemorsa* (Shinners) Cantino and should be placed as a synonym under that taxon. However, if this subspecies were to be recognized at the varietal level, Shimek's name would have priority.

Because Shimek did not designate a type, a lectotype must be selected. The type locality is reported in the protologue as "the sand mound in Muscatine and Louisa counties [Iowa] south of Muscatine." This locality, known today as Big Sand Mound, has been discussed by Brown and Brown (1939) and Guldner (1960). Only four Shimek collections of *Physostegia virginiana* ssp. *praemorsa* from this locality are known to us. None of these are deposited at IA, where Shimek's personal collections are housed. Two of the specimens were collected after the publication of var. *arenaria*. Of the remaining two, the one that corresponds best to the original description is here designated as the lectotype of *Physostegia virginiana* var. *arenaria* Shimek: Iowa, Louisa Co., near Fruitland, sand mound, 25 September 1909, *B. Shimek s.n.*, DAO!

LITERATURE CITED

BROWN, M.E., & BROWN, R.G. 1939 A preliminary list of the plants of the sand mound of Muscatine and Louisa Counties, Iowa. Proc. Iowa Acad. Sci. **46**: 167–178.

CANTINO, P.D. 1982 A mongraph of the genus *Physostegia* (Labiatae). Contr. Gray Herb. **211**: 1–105.

GULDNER, L. F. 1960. The vascular plants of Scott and Muscatine Counties. Davenport Public Museum Bot. Publ. **1**.

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NEW ENGLAND NOTES

CAREX KOBOMUGI OWHI, AN ADVENTIVE SEDGE NEW TO NEW ENGLAND

LISA A. STANDLEY

Carex kobomugi Owhi is a dioecious sand-dune species native to Japan which was first collected in North America by C. W. Townsend in 1929 (Fernald, 1930) and was subsequently discovered on Cape Henry, Virginia, by Frank Egler in 1941. Fernald (1950) reported that it occurred from Ocean County, N.J., to eastern Virginia, although the only collections in herbaria (GH or NY) are from these two localities. Five additional populations from Virginia, and three at Sandy Hook, N.J. are currently known (Stalter, 1980). Naturalized populations of *Carex kobomugi* also occur in New England, at a distance of more than 200 miles north of the New Jersey population. Svenson (1979) reported finding this species in Falmouth, Massachusetts, ca 2 miles inland, in a disturbed sand pit (pers. comm.). *Carex kobomugi* was discovered in Rhode Island in early January, 1982, by Mr. Richard Champlin, and was checked by me on January 25th. This population is located on East Beach, Charleston, Rhode Island, in the Ninigret Conservation Area (Quonochontaug Quadrangle) 1/2 mile east of the parking lot. The main population occupies an area of about 170 m^2 in a blow-out in the primary dune. Both staminate and pistillate plants are present. Scattered plants were found growing in loose sand inshore from the blow-out, and also at about 1 4 mile east of the parking lot. A few individuals of *Ammophila breviligulata* and *Cakile edentula* occurred near the margins of the population.

The plants are quite conspicuous, with coriaceous yellow-green leaves that are 4–6 mm wide, up to 20 cm long, and somewhat contorted. The inflorescence of tightly clustered unisexual spikes forms an oblong head 4–6 cm long which is terminal on a triquetrous culm up to 20 cm tall. The erect, plano-convex perigynia with winged margins and dorsal suture place *Carex kobomugi* in subgenus *Vignea*, although its three stigmas are anomalous in this group. *Carex kobomugi* and the closely related species *C. macrocephala* Willd., which occurs along the Pacific Coast from northern Japan

to Oregon, comprise section *Macrocephalae* Kükenthal. These were not recognized as distinct species in the monographic treatments of Kükenthal (1909) or MacKenzie (1935), despite the numerous, consistent, morphological differences between the western North American northern Japanese and the southern Japanese populations (Table 1). Stacey (1937) clarified the taxonomic history of these two taxa, and confirmed that *Carex kobomugi*, rather than *C. macrocephala*, occurred in eastern North America.

Akiyama (1939) described the differences in foliar anatomy which distinguish these taxa. Leaves of *Carex kobomugi* have a conspicuous multilayered adaxial hypodermis which is not found in *C. macrocephala* (or, to my knowledge, any other species of *Carex*). Leaves of plants from Seaside Park, N.J. and Charleston, Rhode Island have the multiple hypodermis characteristic of *Carex kobomugi* in Japan.

Observations of the East Beach population suggest that *Carex kobomugi* is able successfully to invade disturbed areas of the pri-

Table 1. Morphological differences separating *Carex kobomugi* and *C. macrocephala*.

CHARACTER	*C. kobomugi*	*C. macrocephala*
Perigynium		
orientation	erect	reflexed
shape	elliptical	ovate
shape of base	actute	cordate
margins	entire	lacerate
number of dorsal nerves	ca 20	10–15
number of ventral nerves	ca 20	6–9
Shape of apex of pistillate scales	serrate	entire
Achenes		
length	4–7 mm	3–4.5 mm
shape	oblong, not contorted	elliptical, contorted

mary dunes which result, in many cases, from the destruction of *Ammophila* by trampling. Small (1954) suggested that this species, once established, is able to out-compete *Ammophila*. It would be interesting to evaluate the potential of *Carex kobomugi* to stabilize disturbed dunes, as it appears to survive in sites where *Ammophila* does not, and may provide more resistance to erosion by wind than does *Ammophila*. The range extension of this species may be coincident with increased disturbance of the coastal dunes.

LITERATURE CITED

AKIYAMA, S. 1939. On the systematic anatomy of the leaves of some Japanese Carices. XIX. Bot. Mag. (Tokyo) **53:** 114–118.

FERNALD, M. L. 1930. *Carex macrocephala* and *C. anthericoides*. Rhodora **32:** 9–11.

_____. 1950. Gray's Manual of Botany. 8th edition. D. Van Nostrand. New York.

SMALL, J. A. 1954. *Carex kobomugi* at Island Beach, New Jersey. Ecology **35:** 289–291.

STACEY, J. W. 1937. Notes on *Carex* IX. Leafl. Western Botany **2:** 30–31.

STALTER, R. 1980. *Carex kobomugi* at Sandy Hook, New Jersey. Bull. Torrey Bot. Club **107:** 431–432.

SVENSON, H. K. 1979. The Flora of Cape Cod. Cape Cod Museum of Natural History.

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NOTE ON THE STATUS OF AGALINIS MARITIMA (RAF.) RAF. IN MAINE

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Agalinis maritima (Raf.) Raf. (=*Gerardia maritima*) occurs on salt marshes along the eastern seaboard from Nova Scotia to Florida, Mexico, and the West Indies. It was included in Rare and Endangered Vascular Plant Species in Maine (Eastman, 1978) because there were only three historical Maine records (Wells 1880, Wells 1916, Alna 1966) and there was little contemporary knowledge of the status of the species in the state. In 1981 the Alna site

was relocated and evaluated by the Maine Critical Areas Program staff. The area was registered as a critical area because it was then the only known station extant in Maine. However, the Checklist of Vascular Plants of Maine (Bean, et al., 1966) lists *Gerardia maritima* from Washington and Cumberland Counties as well as York County. In addition, there were unvouchered reports of *A. maritima* present at a number of other localities along the southern Maine coast: Kennebunkport; Winnegance Creek, Phippsburg; Morse River marsh, Phippsburg; Bald Head, Georgetown; Reid State Park, Georgetown; Ocean Park, Old Orchard Beach.

In the summer of 1982 an effort was made to reassess the abundance and distribution of *Agalinis maritima* in southern Maine. During August and September *A. maritima* was found regularly in salt marshes in Kittery Point, York, Wells, Kennebunk, Kennebunkport, Biddeford Pool, Scarborough, Phippsburg and Georgetown. In preliminary searches on more easterly marshes in Warren, South Thomaston, and Winterport, we did not locate *A. maritima* despite the presence of apparently suitable habitat.

Agalinis maritima was most often encountered in the upper salt marsh in slight depressions where the vegetative cover, especially *Spartina patens*, was sparse. The most frequent associates of *A. maritima* were *Glaux maritima, Salicornia europaea, Plantago juncoides, Triglochin maritima, Limonium Nashii*, and occasional *Potentilla anserina* and *Solidago sempervirens*. Seaside Gerardia was often patchily abundant with hundreds of plants in a few square meters. Although Maine individuals are typically shorter (10-15 cm) than plants in southern states, their numbers and seed production seem to indicate that the Maine populations are thriving and likely to persist.

Due to its small size *Agalinis maritima* is not conspicuous on the marsh until it blooms. Its blossoms are short-lived, often falling off within a day. These factors, coupled with its annual habit, locally transient and patchy distribution, and the fact that it grows on salt marshes, a habitat infrequently visited by some botanists, make it likely that Seaside Gerardia is a species more overlooked and underreported than genuinely rare in Maine. At least, it is a frequent member of the flora of most salt marshes along the southern Maine coast. The northeastern limit of the Maine distribution of *A. maritima* remains to be discovered.

LITERATURE CITED

BEAN, RALPH C., CHARLES D. RICHARDS, FAY HYLAND. 1966. Revised Checklist of the Vascular Plants of Maine. Bulletin of Josselyn Botanical Society of Maine. No.8, Orono, Maine.

EASTMAN, L. M. 1978. Rare and Endangered Vascular Plant Species in Maine. Prepared by the New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service (Newton Corners, MA).

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LITERATURE FOR NEW ENGLAND BOTANISTS

CAMPBELL, CHRISTOPHER S. and LESLIE M. EASTMAN, 1980. *Flora of Oxford County, Maine*. 244 pp., biblog., index. Orono, Maine, Life Sciences and Agricultural Experiment Station, University of Maine, Technical Bulletin **99**.

If each county in New England had a flora like this outstanding one, we would approach the English in their study of local botany—alas we are far from this ideal. Campbell and Eastman have used Arthur Stanley Pease's excellent *Flora of Northern New Hampshire* (1964) as a model for their flora, and they have produced a solid work. A 29-page introduction discusses pertinent geographical features of the area and details the various plant associations. The occurrence of the taxa is documented with thoroughness of citation of herbarium specimens on a town by town basis. Frequency, and brief habitat notes are included for each species.

MCDONNELL, MARK J. 1979. *The Flora of Plum Island, Essex County,* Massachusetts. 110 pp., bibliogr., index. Durham NH, New Hampshire Agricultural Experiment Station, University of New Hampshire, Station Bulletin **513.**

Maps, diagrams, and a description of the geographical features (climate, geology, land-use history), and plant associations preface this flora. Plum Island is an area long of interest to New England naturalists—especially birders and tide-marsh students. McDonnell's flora summarizes and adds to the previous botanical collections and studies of the island. It provides for the first time a proper base for further additions and for documenting future coastal vegetation changes.

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BOOK REVIEW

KUIJT, JOB. 1982. *A Flora of Waterton Lakes National Park*. xxiv + 684 pp. University of Alberta Press, Edmonton, Alberta. (Price $25; $15, waterproof paperback)

This handsome flora should be of great use to botanists and botanically oriented visitors to Waterton Lakes Park and beyond to Glacier Park, east of the Continental Divide, and the Alberta Rockies south of latitude 50°. Further, 55% of the total species occuring in Alberta Province occur in the Park Flora, so the book is useful over a wide area.

The introduction contains a brief description of the Park geology and the plant communities. There are 18 pages of master keys designed to lead one to the proper plant family. There are further keys to the genera within the family section and species keys under the genus description. Families, genera, and species are all arranged alphabetically, a feature that has both merits and drawbacks. The text is clearly written, and full; measurements are included, though technical terms are kept to a minimum to facilitate use by the interested public. Each species is illustrated by a line drawing showing habit, and occasionally, details. The book concludes with a glossary, bibliography, and index.

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BOOK REVIEW

BENSON, LYMAN. 1982. *The Cacti of the United States and Canada*. ix + 1044 pp. Stanford, CA., Stanford University Press. (Price $85.)

The Cacti of the United States and Canada is a monument to a life-time of research on the subject, and what a monument! One

opens the book expecting a short introduction to a descriptive monograph. This introduction (i.e. Part I) turns out to be a book in its own right, a 247 page, most readable treatise on all aspects of the biology, taxonomy, and ecology of cacti. It includes a long section on the floras and floristic associations of the United States and Canada, listing the marker species (usually woody) plus the more important cactus species in each. A New England botanist browsing through Part 1 will quickly learn more about cacti than he ever knew before.

Part 2 begins with interpretive notes to understanding the text and a key to the genera of Cactaceae. The text gives a comprehensive description of the 18 genera, 151 species, and 133 varieties which Benson recognizes as growing in this region. The descriptions include full technical details, large-scale range maps, numerous black and white photographs and 194 in color; and marvellous detailed line-drawings for many species by Lucretia B. Hamilton. There are keys to the species, and tables comparing the varietal characters. Next is a 60 page section of documentation for the scientific names. (Benson has reduced many species to varieties.) The book concludes with a glossary, references, illustration credits, reference maps, and an index.

In the Introduction (p. 8) under a photograph of George Engelmann is a statement that he was an "astute botanist and the most outstanding student of cacti of all time". Readers of this book will surely add ". . .until the advent of Lyman Benson."

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1983 SINO-AMERICAN BOTANICAL EXPEDITION TO WESTERN SICHUAN PROVINCE

Three U.S. botanists have been invited to participate in a joint Chinese-American botanical expedition to western Sichuan Province, People's Republic of China, in late summer and early fall of this year. The expedition will be conducted under the auspices of the Botanical Society of America's Committee for Scientific Liaison with the P.R.C. and both the Institute of Botany, Beijing, and the Chengdu Institute of Biology, with the sponsorship of Academia Sinica. The expedition will visit Mt. Emei (Mt. Omei) and the Wolong Nature Reserve. The U.S. participants will try to fill specific requests for research material (living plants, seeds, herbarium specimens, pickled material, wood samples, etc.) from this part of China. Requests for material can be sent to any of the three American participants: Bruce Bartholomew, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118; David E. Boufford, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138; and Paul L. Redfearn, Jr., Department of Life Sciences, Southwest Missouri State University, Springfield, MO 65802.

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Manuscripts should be submitted in **triplicate** (an original and two xerox copies) and **must be double-spaced** (at least 3 8 of an inch) **throughout** including footnotes, figure legends, and references. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distributions. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S.R. Hill, Rhodora 84: 1 83, 159 264, 317 409, 1982, particularly with reference to indentation of keys and synonyms. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503 548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual*, 3rd ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 x 6 inches, be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1 2 x 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size.

Contrary to prior policy, Rhodora now requests that an *abstract* and a list of key words be supplied with all papers submitted except for very short articles and notes.

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Rhodora

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Cover illustration

Trollius laxus Salisb. is very rare as it nears its northeastern limit in Connecticut. Some old records indicate that it has grown in parts of New Hampshire and Maine, so it may yet be found in appropriate habitat.

Original artwork by Tess Feltes, Illustrator.

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THE COMPOSITION AND SEASONAL PERIODICITY OF THE MARINE-ESTUARINE CHLOROPHYCEAE IN NEW HAMPSHIRE[1]

ARTHUR C. MATHIESON AND EDWARD J. HEHRE

In two previous accounts we have summarized a variety of floristic and phenological data on the Rhodophyceae (Hehre & Mathieson, 1970) and Phaeophyceae (Mathieson & Hehre, 1982) of New Hampshire. A similar compilation for the marine Chlorophyceae is given here, based upon collections and observations made from 1965 to 1980. Monthly or seasonal collections of green algae were made at numerous estuarine and coastal sites throughout New Hampshire (Figs. 1 and 2), with herbarium voucher specimens of each taxon being prepared and deposited in the Albion R. Hodgdon Herbarium of the University of New Hampshire (NHA). The recent nomenclature of South (1976) is followed in most cases. In the present account, a synopsis of 58 chlorophycean taxa is given, with a statement of relative abundance, local distribution (vertical and horizontal), and seasonal occurrence of each taxon.

PHENOLOGY AND DISTRIBUTION

The monthly occurrence of chlorophycean taxa within estuarine-coastal waters in New Hampshire is summarized in Table I. The lowest numbers of taxa were recorded in December and January (i.e., 27 and 24 taxa respectively), while the highest numbers were

[1]Scientific Contribution No. 1148 from the New Hampshire Agricultural Experiment Station; also issued as Contribution Number 120 from the Jackson Estuarine Laboratory.

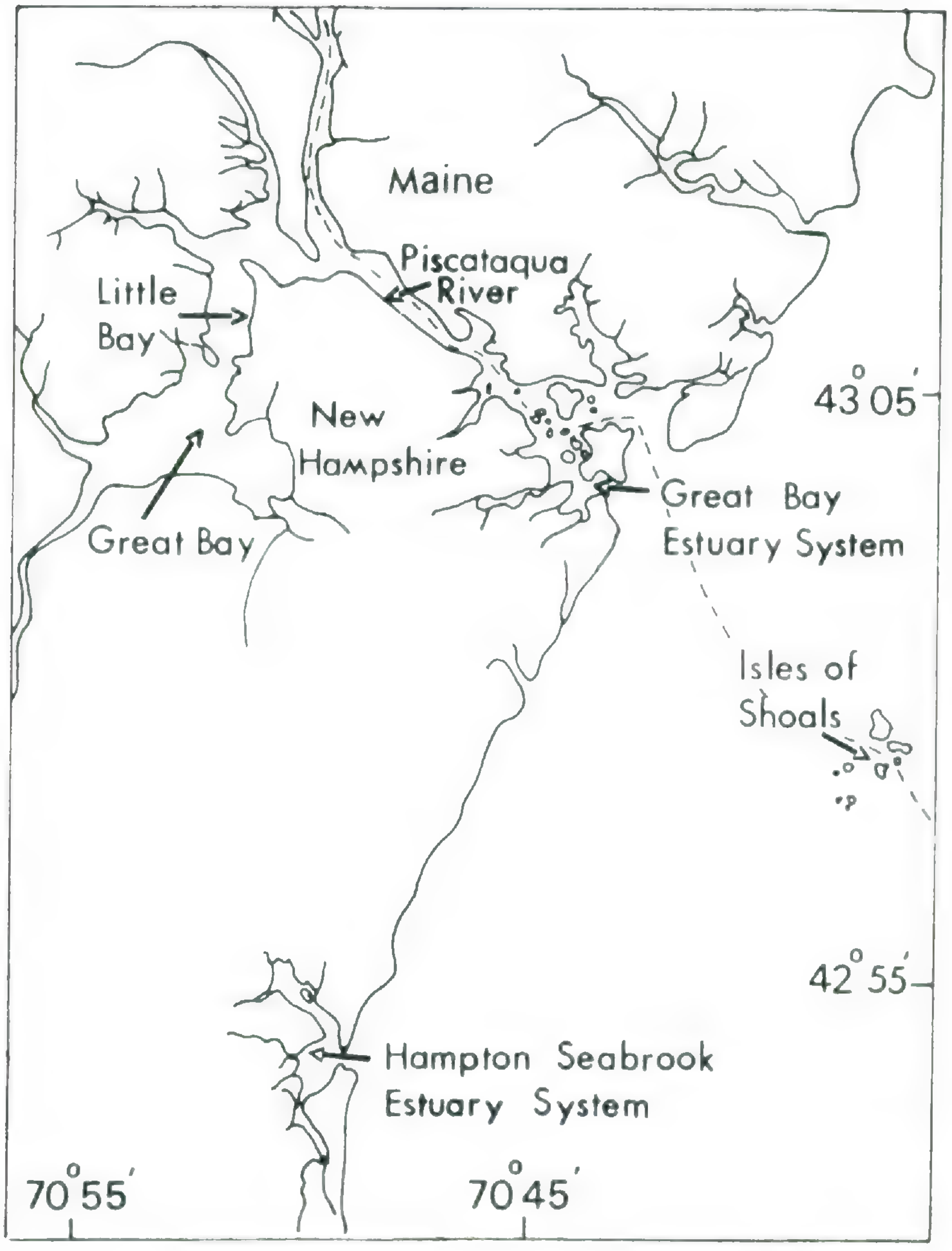

Figure 1. The New Hampshire coastal zone

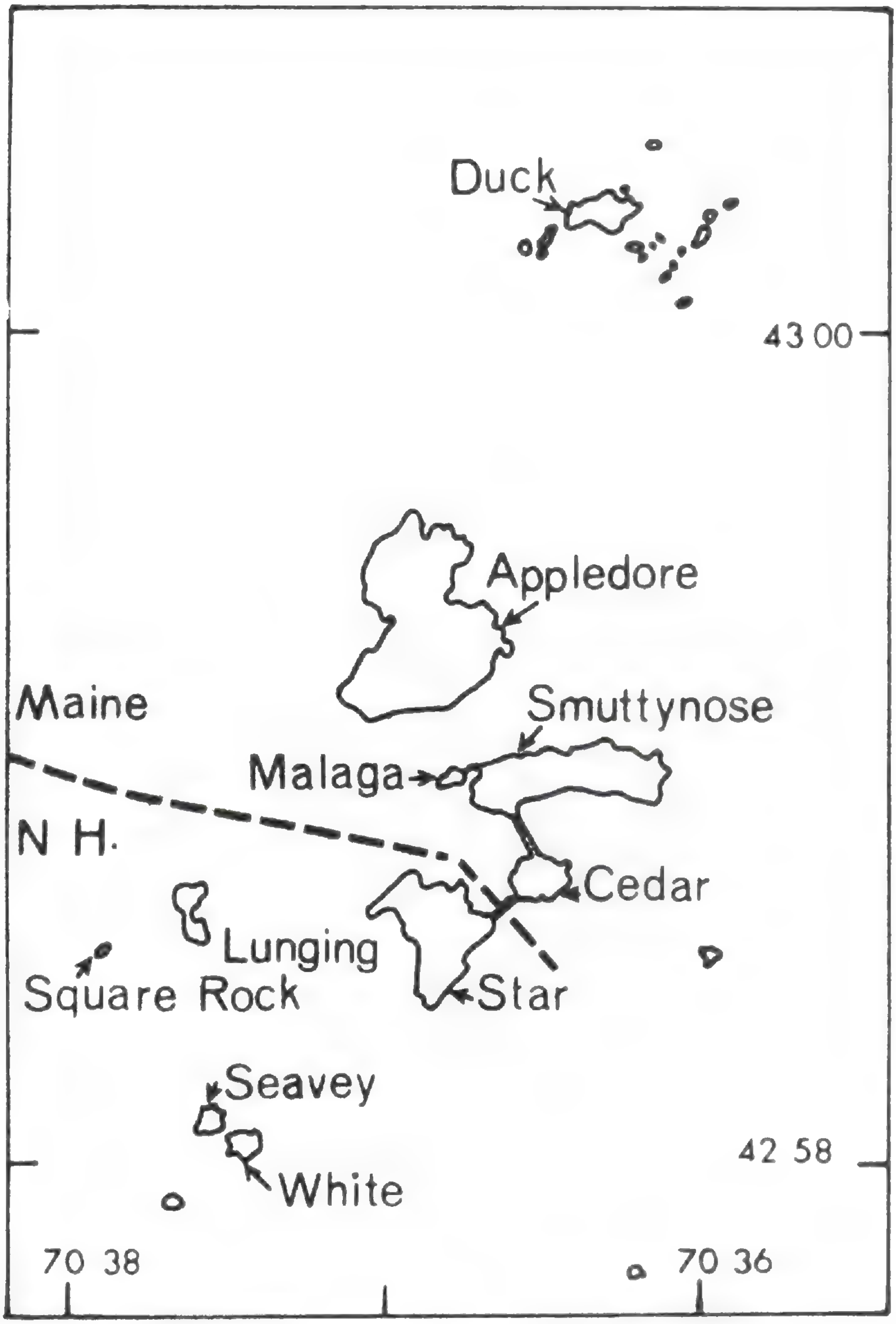

Figure 2. The Isles of Shoals, New Hampshire — Maine

found in July and August (43 and 40 taxa, respectively). A few fresh-water green algae (*Microspora, Oedogonium, Spirogyra* and *Stigeoclonium* spp.) were collected intermittently throughout the year and primarily in riverine or innermost estuarine habitats.

Forty-eight (83%) of the green algae recorded were considered to be annuals, while only 7 taxa (12%) were interpreted as perennials (Fig. 3). The longevity designations for *Cladophora sericea, Derbesia marina,* and *Ulva lactuca* require further study, as they may be either aseasonal annuals or pseudoperennials (*sensu* Knight & Parke, 1931). Specific details on the longevity and seasonal occurence of each taxa are summarized in Table I, as well as in the following annotated checklist.

A summary of the local distribution of chlorophycean taxa in the four major coastal-estuarine areas in New Hampshire (Figs. 1 and 2) is also shown in Figure 3. The highest number of species was recorded from the near-shore open coast between Portsmouth and Seabrook (i.e. 47 taxa). The species diversity within the Great Bay System and at the Isles of Shoals were very similar (i.e. 46 and 42 taxa, respectively). In contrast to the similarity of species richness at the three areas, their species compositions were quite different (Table I). For example, the fresh-water green algae mentioned earlier were only collected within riverine (i.e. innermost estuarine) habitats of the Great Bay Estuary System, and they were absent at both open coastal sites. The low species diversity (i.e. 18 taxa) within the Hampton-Seabrook Estuary System contrasts strongly with that of the Great Bay Estuary System.

ANNOTATED CHECKLIST

Fifty-eight taxa of chlorophycean algae are recorded in the following checklist from coastal and estuarine environments within the state. Twelve of these plants are newly recorded from New Hampshire: *Acrochaete repens, Bolbocoleon piliferum, Chlorochytrium moorei, Cladophora albida, C. pygmaea, C. rupestris, Enteromorpha flexuosa* ssp. *flexuosa, Gomontia polyrhiza, Monostroma leptodermum, Prasinocladus marinus, Pringsheimiella scutata* and *Stichococcus marinus*. None of the above taxa represent range extensions on the northeast coast of North America. The new records are indicated by asterisks in the list.

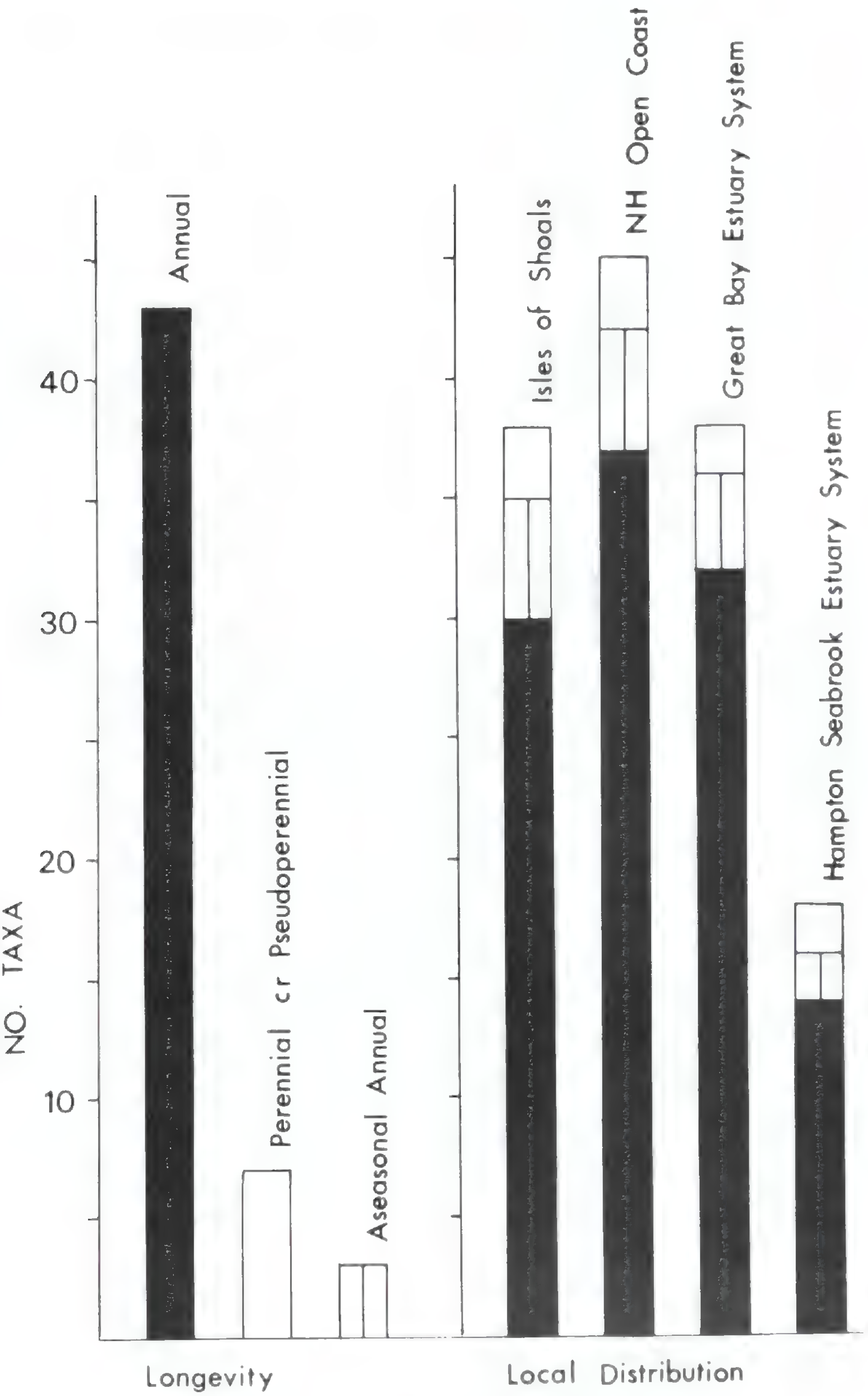

Figure 3. The longevity and local distribution of chlorophycean taxa in New Hampshire

Table 1: **Seasonal Occurrence, Longevity, and Local Distribution of Chlorophyceae**

TAXA	MONTHS												
	J	F	M	A	M	J	J	A	S	O	N	D	
Acrochaete repens			X*				X*						Ann. 2*,4*
Acrochaete viridis	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. 1,2,4
Blidingia minima	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. 1–4
Bolbocoleon piliferum			X*				X*						Ann. 2*
Bryopsis plumosa		X**				X	X	X	X	X	X	X	Ann. 1 4
Capsosiphon fulvescens			X*		X	X	X	X	X	X	X		Ann. 2,4
Chaetomorpha aerea	X	X	X	X	X	X	X	X	X	X	X	X	Per. 1,2,4
Chaetomorpha brachygona	X		X		X	X	X	X	X	X	X	X	Ann. (?) 1,2,4
Chaetomorpha linum	X	X	X	X	X	X	X	X	X	X	X	X	Per. 1–4
Chaetomorpha melagonium	X	X	X	X	X	X	X	X	X	X	X	X	Per. 1,2,4
Chaetomorpha minima										X	X		Ann. (?) 1
Chaetomorpha picquotiana	X	X	X	X	X	X	X	X	X	X	X	X	Per. 1–4
Chlorochytrium moorei										X			Ann. 2
Cladophora albida		X	X	X		X	X	X				X	AAnn. 1,2,4
Cladophora pygmaea	X	X	X	X	X	X	X	X	X	X			Per. 4
Cladophora refracta							X	X		X			Ann. 1,4
Cladophora rupestris		X				X		X		X			Per. 1
Cladophora sericea	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. or PPer. 1 4
Codiolum gregarium							X*	X			X		Ann. 2,4
Codiolum petrocelidis			X					X					Ann. 1,2
Codiolum pusillum		X				X	X	X	X	X	X	X	Ann. 1,2,4*

Derbesia marina				X	X						X		AAnn. or PPer. 1,2
Enteromorpha clathrata				X		X	X	X	X	X	X	X	Ann. 1 4
Enteromorpha compressa	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. 1 4
Enteromorpha flexuosa ssp. *flexuosa*							X		X	X			Ann. 4
Enteromorpha flexuosa ssp. *paradoxa*		X		X			X	X	X	X	X	X	Ann. 1 4
Enteromorpha intestinalis	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. 1 4
Enteromorpha linza	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. 1 4
Enteromorpha prolifera	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. 1 4
Enteromorpha torta				X			X	X	X			X	Ann. 2,4
Entocladia flustrae		X		X		X							Ann. (?) 1,2
Gomontia polyrhiza			X					X					Ann. (?) 1,2
Halicystis ovalis							X						Per. (?) 2
Microspora pachyderma	X	X	X	X	X	X*	X*			X	X*		Ann. 2*,4
Monostroma fuscum	X	X	X	X	X	X	X	X	X	X	X	X	Ann. 1 4
Monostroma grevillei	X	X	X	X	X	X				X	X	X	Ann. 1 4
Monostroma leptodermum					X	X	X	X	X				AAnn. 2 4
Monostroma oxyspermum	X	X	X	X	X	X	X	X	X	X	X	X	Ann. 1 4
Monostroma pulchrum			X	X	X	X							Ann. 1,2,4
Mougeotia sp.							X						Ann. 4
Oedogonium sp.								X	X				Ann. 4
Percursaria percursa		X	X	X	X	X	X	X	X	X	X		AAnn. 1 4
Prasinocladus marinus							X*						Ann. 2*

Table 1 (cont.)

TAXA	MONTH												
	J	F	M	A	M	J	J	A	S	O	N	D	
Prasiola stipitata	X	X	X	X	X	X	X	X	X	X	X		AAnn. 1,2,4
Pringsheimiella scutata			X							X			Ann. (?) 1
Pseudendoclonium submarinum							X	X			X		AAnn. 1,4
Rhizoclonium riparium	X	X	X	X	X	X	X	X	X	X	X		AAnn. 1-4
Rhizoclonium tortuosum	X	X	X	X	X	X	X	X	X	X	X		AAnn. (?) 1,2,4
Spirogyra sp.							X						Ann. 4
Spongomorpha arcta		X	X	X	X	X	X	X	X	X	X	X	Ann. 1,2,4
Spongomorpha spinescens				X	X	X	X	X		X	X	X	Ann. 1,2,4
Stichococcus marinus						X							Ann. 1
Stigeoclonium sp.			X										Ann. 4
Ulothrix flacca	X	X	X	X	X	X		X			X	X	Ann. 1,2,4
Ulva lactuca	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. or PPer. 1-4
Urospora penicilliformis	X	X	X	X	X	X	X	X		X	X	X	Ann. 1,2,4
Urospora speciosa		X	X	X	X								Ann. 1,2,4
Urospora wormskioldii	X	X	X	X	X		X	X*				X	Ann. 1,2,4
	24	32	36	34	32	36	43	40	30	36	34	27	

KEY TO TABLE I

x = presence
* = obtained in culture
** = residual basal material

Longevity:
- Ann. = annual
- AAnn. = aseasonal annual
- Per. = perennial
- PPer. = pseudoperennial *sensu* Knight & Parke (1931)

Local Distribution:
- 1 = Isles of Shoals
- 2 = Near-shore open coast
- 3 = Hampton-Seabrook Estuary System
- 4 = Great Bay Estuary System

***Acrochaete repens** N. Pringsheim

Obtained in cultures from open coastal and estuarine water samples (March and July), which were concentrated on glass fiber filters and grown in enriched seawater media (12-32 0/00) at 6-20C (R. Zechman, personal comm.). No *in situ* populations seen. Annual.

Acrochaete viridis (Reinke) R. Nielsen

Common on the open coast, less abundant and scattered within the Great Bay Estuary System. Endophytic within several fleshy red algae (0 to -8m), often turning them green. Nielsen (1979) transferred the type species of *Entocladia* Reinke to *Acrochaete* based upon culture studies of materials from the type locality. Aseasonal annual.

Blidingia minima (Nageli *ex* Kützing) Kylin

A common "opportunitistic" species (see Prange, 1978) at diverse open coastal and estuarine sites. Growing on a variety of substrata (rock, wood, etc.). More abundant and exhibiting a broader zonation in estuarine (+1.0 to +2.3m) than open coastal areas (+2.0 to +2.5m). Plants found in riverine (i.e. innermost estuarine) sites are morphologically variable and should be designated as variety *subsalsa* (Kjellman) Scagel, while the unbranched coastal plants are referrable to variety *minima* (see Abbott & Hollenberg, 1976; Scagel, 1966). Norris (1971) suggests that *Blidingia marginata* may be a juvenile stage of *B. minima*: we agree and have not differentiated it here. Aseasonal annual.

***Bolbocoleon piliferum** N. Pringsheim

Obtained in cultures from open coastal water samples (March and July), which were concentrated on glass fiber filters and grown in enriched sea water (12–32 0/00) at 6–20C (R. Zechman, personal comm.). None of the cultured plants occurred as endophytes or epiphytes, although a variety of "host" plants were present in the same cultures. No *in situ* populations seen. Annual.

Bryopsis plumosa (Hudson) C. Agardh

Common in shallow estuarine areas, rare on the open coast. Found on rocks, shells and coarse algae (0.0 to −10m). Abundant

during the summer and with some residual plants occasionally found during the fall-winter. Annual.

Capsosiphon fulvescens (C. Agardh) Setchell *et* Gardner

Occasional, found on a variety of substrata (+2.2 to +2.7m) in riverine or innermost estuarine habitats — often at the head-waters of tidal streams. Rare on the open coast, found growing in marshy ponds or pools, mixed with *Enteromorpha* spp., *Cladophora sericea*, and *Rhizoclonium riparium*. Collected from May-November. Annual.

Chaetomorpha aerea (Dillwyn) Kützing

Common on the open coast and collected at one outer estuarine site on the Piscataqua River. Found on rocks and ledges (+1.0 to +1.8 m), usually in tide pools. Often epiphytized by *Monostroma* spp., *Protectocarpus speciosus*, diatoms and other algae. Blair, et al. (1982) give a detailed account of the taxon as well as its differentiation from *C. linum*. Perennial.

Chaetomorpha brachygona Harvey

Occasional at several open coastal sites and scattered within the Great Bay Estuary System. Often mixed with other unbranched cladophoralean algae (+0.6 to −18.0m). Blair (1983) gives a detailed account of the taxon, as well as its differentiation from *Chaetomorpha cannabina* and *C. capillaris*. Annual (?).

Chaetomorpha linum (O. F. Müller) Kützing

Common in open coastal and estuarine environments; found detached and entangled amongst coarse seaweeds, including *Chaetomorpha picquotiana* (+0.6 to −20.0m). Occasionally found attached (i.e. initially) by a single basal cell (Blair, 1983). More common than *C. picquotiana* in estuarine areas, where it often forms extensive festoons 3–5 m long in tidal rapids (Reynolds, 1971). Perennial.

Chaetomorpha melagonium (Weber *et* Mohr) Kützing

Common on the open coast; rare within the Great Bay Estuary System where it often occurs as single filaments versus clumps of filaments on the open coast (Reynolds & Mathieson, 1975). Found on rocky substrata (+0.6 to −26.0m), often in tide pools. Rare in estuarine sites. Perennial.

Chaetomorpha minima Collins *et* Hervey

Found a few times at the Isles of Shoals during October and November; growing attached by a basal cell to *Chaetomorpha aerea* and *C. melagonium* (0.0 to +1.0m). Blair (1983) characterizes the taxon and discusses its possible interrelationships with *Rhizoclonium riparium*. Annual (?).

Chaetomorpha picquotiana (Montagne) Kützing

Common on the open coast, occasional and scattered in estuarine sites (Blair, 1983). Forming entangled masses amongst coarse seaweeds (+0.6 to −20.0m), including *Chaetomorpha linum*. Blair (1983) gives a recent interpretation of this taxon which has previously been referred to as *C. atrovirens* (Taylor, 1962).

***Chlorochytrium moorei** Gardner

Found once (October) growing within the mucilaginous sheath of the colonial diatom *Berkeleya rutilans*. Present in a high (+2.0m) marshy tide pool on the open coast. Annual.

***Cladophora albida** (Hudson) Kützing

Occasional at scattered open coastal and estuarine sites. Epilithic or epiphytic on coarse algae (0.0 to −3.0m). Present year-round. Aseasonal annual.

***Cladophora pygmaea** Reinke

Occasional at scattered sites within the Great Bay Estuary System. Found on rocks in association with a variety of encrusting taxa (e.g. *Pseudolithoderma extensum, Hildenbrandia rubra, Rhodophysema elegans, Ralfsia* spp.) within the sublittoral zone (0 to −10m). The plant may have been missed on the open coast because of its small size and dark green color (see South & Hooper, 1980; Wilce, 1970). Perennial.

Cladophora refracta (Roth) Kützing

Occasional on rocks at the Isles of Shoals (+2.0 to +2.5m), sometimes in tide pools. Found once within the mid-eulittoral zone within the Great Bay Estuary System. Annual.

***Cladophora rupestris** (Linnaeus) Kützing

Occasional on rocks at the Isles of Shoals (0.0 to −1.0 m) — often in

tide pools. Reported by Collins (Hoek, 1981) from Hampton, near the southern border of the near-shore open coast of New Hampshire. To date we have only collected the plant from the near-shore open coast in Massachusetts and Maine. Perennial (?).

Cladophora sericea (Hudson) Kützing

Common at diverse open coastal and estuarine sites. Growing on a wide variety of substrata (+2.6 to −6.0m). An aseasonal annual or a pseudoperennial (Knight & Parke, 1931) which is capable of regenerating upright filaments from basal, residual filaments.

Codiolum gregarium A. Braun

Occasional on the open coast and at the mouth of the Great Bay Estuary System. Also obtained in culture from estuarine water samples (July), which were concentrated on glass fiber filters and grown in enriched seawater media (12–32 0/00) at 6–20C (R. Zechman, personal comm.). The *in situ* collections were found on rocks within the splash zone (+2.0 to +3.4m) of the open coast, often mixed with a variety of blue-green algae (*Calothrix scopulorum, Lyngbya* and *Oscillatoria* spp.). The morphology of *Codiolum gregarium* is only slightly different from *C. pusillum* (Hanic, 1965), and both of these plants represent stages in the life histories of *Urospora* spp. and other green algae (Kornmann, 1959; Kornmann & Sahling, 1977; Scagel, 1966). Annual.

Codiolum petrocelidis Kuckuck

Occasional on the open coast, endophytic within *Petrocelis middendorfii* (0.0 to −8.0m). The plant is described as the "sporophyte" generation of *Spongomorpha spinescens* (Jonsson, 1958; Scagel, 1966). Annual.

Codiolum pusillum (Lyngbye) Kjellman

Common on the open coast. Also obtained in culture from estuarine water samples (July), which were concentrated on glass fiber filters and grown in enriched seawater media (12–32 0/00) at 6–20C (R. Zechman, personal comm.). The *in situ* collections were found on high rocks (+2.0 to +3.4m) during the summer and fall; often mixed with *Calothrix scopulorum, Urospora* spp., *Ulothrix flacca,* and *Bangia atropurpurea*. As noted previously, the plant is very similar morphologically to *C. gregarium*; both plants represent

stages in the life history of *Urospora* spp. (Hanic, 1965; Kornmann & Sahling, 1977; Scagel, 1966) and other green algae. Annual.

Derbesia marina (Lyngbye) Solier

Occasional on the open coast. Found on rocks (often sponge covered) within the sublittoral zone (0 to −15m). The plant represents the sporophytic stage in a pleomorphic (specialized heteromorphic) life history involving gametophytic *Halicystis ovalis* (Sears & Wilce, 1970). The vesicular stage of New England material has only been obtained in culture from Massachusetts plants (Sears, 1971) and from natural populations in New Hampshire (Mathieson & Burns, 1970). An aseasonal annual or a pseudoperennial, which is capable of regenerating from residual materials in sponge tissue (Sears, 1971).

Enteromorpha clathrata (Roth) Greville

Abundant in estuarine areas, entangled amongst coarse plants or attached to a variety of substrata (+1.0 to +2.0m). Less abundant on the open coast, occurring in high tide pools (+2.0 to +2.7m) mixed with *Enteromorpha* spp., *Cladophora sericea*, and *Rhizoclonium riparium*. Collected from April-December. Aseasonal annual.

Enteromorpha compressa (Linnaeus) Greville

Abundant at several widely distributed estuarine sites; less common on the open coast. Growing on rocks, occasionally epiphytic (+1.5 to +2.5m). As noted by DeSilva and Burrows (1973) the plant is extremely variable morphologically. Present year-round. Aseasonal annual.

***Enteromorpha flexuosa** (Wulfen *ex* Roth) J. Agardh
subsp. **flexuosa** Bliding

Uncommon at a few sites within the Great Bay Estuary System. Exposed to considerable fresh water. Found on rocks and entangled amongst coarse algae (+2.5m). Annual.

Enteromorpha flexuosa (Wulfen *ex* Roth) J. Agardh subsp. **paradoxa** (Dillwyn) Bliding

Occasional, found attached and entangled in high marshy tide pools (+2.2 to +2.7m) on the open coast, often mixed with *Entero-*

morpha clathrata, Cladophora sericea and *Rhizoclonium riparium*. More abundant in estuarine than coastal areas, particularly in high marshy pannes in the former areas. Primarily collected during the summer and fall. Annual.

Enteromorpha intestinalis (Linnaeus) Link

Abundant, found on a variety of substrata (0.0 to +2.5m). Present in tide pools and in disturbed surfaces (see Daly & Mathieson, 1977) on the open coast, as well as widely distributed in estuarine and riverine locales. Present year-round. Aseaonsal annual.

Enteromorpha linza (Linnaeus) J. Agardh

Common on the open coast, occasional and widely distributed in estuarine sites. Found on a variety of solid substrata, as well as epiphytic on coarse algae (+0.5 to −12.0m). Present year-round. Aseasonal annual.

Enteromorpha prolifera (O. F. Müller) J. Agardh

Occasional on the open coast; found on a variety of substrata, as well as entangled in high marshy areas (+1.0 to +2.7m). Ubiquitous in estuarine and riverine areas, again on a variety of substrata (+1.0 to 2.0m). Extremely variable morphologically, and often mixed with a variety of other *Enteromorpha* species. Present year-round. Aseasonal annual.

Enteromorpha torta (Mertens *in* Jurgens) Reinbold

Occasional in outer estuarine sites within the Great Bay Estuary System and on the adjacent open coast. Found on rocks and entangled amongst coarse algae (+1.5 to +3.0m). Mixed with other *Enteromorpha* spp., *Cladophora sericea*, and *Rhizoclonium riparium*. According to Nienhuis (1969) the morphological plasticity of *E. prolifera* may overlap with *E. torta* and the taxonomic difference between the two may not always be clear. Annual.

Entocladia flustrae (Reinke) Batters

Common on the open coast. Growing on the chitinous skeletons (i.e. hydrotheca) of *Sertularia* sp. (−0.3 to +2.2m) — often on vertical rock faces. Although only collected occasionally, it can probably be collected whenever it is specifically looked for (cf South & Hooper, 1980). Annual.

***Gomontia polyrhiza** (Lagerhiem) Bornet *et* Flahault

Uncommon, found twice (March and August) within mollusk shells on the open coast (0.0 to +2.0m). Probably more common than our collections indicate. The plant is described as the sporophytic generation of *Monostroma grevillei* (Kornmann, 1959). Annual (?).

Halicystis ovalis (Lyngbye) Areschoug

Uncommon, found twice during July at a single open coastal site; this is the only *in situ* collection of the plant on the northeast coast of North America (Mathieson & Burns, 1970). The vesicular thallus, which is the gametophytic stage in the life history of *Derbesia marina* (Sears & Wilce, 1970), is found attached to a variety of crustose coralline algae (e.g. *Clathromorphum circumscriptum, Lithothamnium glaciale,* and *Phymatolithon lenormandii*), on large rocks and boulders that are relatively free of sand or silt (−12 to −24m). According to Scagel (1966) new vesicles can be regenerated on successive years from the residual rhizomes. Perennial.

Microspora pachyderma (Wille) Lagerheim

Common on rocks at the head-waters of tidal tributaries (i.e. riverine sites) and occasionally found in more estuarine areas during spring thaw. The plant has also been extensively obtained in estuarine and open coastal water samples (June, July and November) which were concentrated on glass fiber filters and grown in enriched sea water (12–32 0/00) at 6–20C (R. Zechman, personal comm.). A fresh-water green alga that has tentatively been identified as *M. pachyderma*, although it has not been identified previously from estuarine habitats (Collins, 1912; Prescott, 1962). Found mixed with *Cladophora sericea* and *Blidingia minima* var. *subsalsa* (+1.5 to +2.0m) during January to May, and with a single *in situ* collection obtained in October. Annual.

Monostroma fuscum (Postels *et* Ruprecht) Wittrock

Common at a variety of open coastal and estuarine sites. Growing on rocks and epiphytic on coarse algae (+0.45 to −24.0m), often in tide pools. Present year-round and probably represented by several isomorphic sporophytic and gametophytic generations (Dube, 1967). Annual.

Monostroma grevillei (Thuret) Wittrock

Common at a variety of open coastal and estuarine sites; less abundant in the latter than the former areas. Found on rocks, mussels and as an epiphyte on coarse algae (+1.7 to −6.0m). First occurs as a saccate stage during the fall. Abundantly reproductive in May and June and absent during July-September. The interrelationship between *Gomontia polyrhiza* and *Monostroma grevillei* has been previously noted (see Kornmann, 1959). Annual.

***Monostroma leptodermum** Kjellman

Abundant at outer estuarine sites — rare on the open coast. Usually epiphytic on *Zostera marina* (0.0 to −1.0m). Found from May to September. Annual.

Monostroma oxyspermum (Kützing) Doty

Common in estuarine areas and tolerant to pronounced salinity variations. Rare and only collected a few times on the open coast —particularly after a very warm summer. Found on wood as well as as epilithic and epiphytic (+1.0 to +2.5m). Most abundant during the summer but some residual populations survive periods of winter ice coverage. Annual.

Monostroma pulchrum Farlow

Common in open coastal and outer estuarine areas within the Great Bay Estuary System. Epiphytic on coarse algae (+1.0 to −1.3m). Collected during March-June, with reproductive plants abundant during May and June. Annual.

Mougeotia sp.

Collected once (July) on rocks at the head-waters of the tidal limits of the Oyster River (+1.5 to +2.0m). A fresh-water green alga, found mixed with *Spirogyra* sp., *Cladophora sericea, Enteromorpha prolifera* and *Blidingia minima* var. *subsalsa*. Annual.

Oedogonium sp.

Collected twice (August and September) on rocks beneath a waterfall at the head-waters of the tidal limits of the Oyster River (+2.0m). A fresh-water green alga, found mixed with *Cladophora sericea, Enteromorpha prolifera* and *Blidingia minima* var. *subsalsa*. Annual.

Percursaria percursa (C. Agardh) Rosenvinge

Common in estuarine areas, occasional on the open coast (+2.0 to +2.7m). Growing amongst emergent halophytic plants in estuarine areas, mixed with *Enteromorpha* spp., *Cladophora sericea*, and *Rhizoclonium riparium*. Found in high marshy tide pools on the open coast, mixed with similar green algae as in estuarine areas. Most abundant during the summer, but present year-round. Annual.

***Prasinocladus marinus** (Cienkowski) Waern

Obtained in cultures from open coastal water samples (July), which were concentrated on glass fiber filters and grown in enriched seawater media (32 0/00) at 6C (R. Zechman, personal comm.). The dichotomously branched colonial form was observed growing detached on the surface of the culture media. No *in situ* populations seen. Annual.

Prasiola stipitata Suhr *in* Jessen

Common on the open coast and at the mouth of the Great Bay Estuary System. Often forming a conspicuous green coating in crevices and pockets on high rock faces (+2.7 to +3.5m), often associated with bird droppings. Present year-round. Aseasonal annual.

***Pringsheimiella scutata** (Reinke) Marchewianka

Rare, found twice on the open coast (+0.5 to +1.5m), once epiphytic on *Chondrus crispus* another time on *Choreocolax polysiphoniae*. Annual (?).

Pseudendoclonium submarinum Wille

Occasional in open coastal and estuarine areas. Found on rocks and shells (+2.0 to −10.0m). Probably more abundant than our collections would indicate. Aseasonal annual (Sears, 1971).

Rhizoclonium riparium (Roth) Harvey

Common in estuarine locations (+1.5 to +2.7m) and high marshy tide-pools (+2.2 to +2.7m) on the open coast, mixed with *Cladophora sericea* and *Enteromorpha* spp. Most common during the summer, but present year-round. Nienhuis (1975) placed *R. implexum* (Dill.) Kutz. (=*R. kerneri*) in synonomy with *R. riparium* based on extensive field and culture studies. Aseasonal annual.

Rhizoclonium tortuosum Kützing

Common on the open coast and with scattered estuarine populations within the Great Bay Estuary System. Found entangled amongst coarse algae (+0.6 to −12.0m). Most abundant during the summer, but present year-round. Aseasonal annual (?). See Blair (1983) for a detailed account of the taxon.

Spirogyra sp.

Collected once (July) on rocks at the head-water of the tidal limits of the Oyster River (+1.5 to +2.0m). A fresh-water green alga, found mixed with *Mougeotia* sp., *Cladophora sericea, Enteromorpha prolifera* and *Blidingia minima* var. *subsalsa*. Annual.

Spongomorpha arcta (Dillwyn) Kützing

Common on the open coast and outer sites within the Great Bay Estuary System. Usually epilithic, occasionally epiphytic on coarse seaweeds or entangled amongst dense populations of *Mytilus edulis* on the open coast (+0.9 to −11.0m). Most abundant during the winter and spring, but present year-round. Lamb and Zimmerman (1964) suggest that the plant is a perennial or pseudo-perennial being represented by reduced or inconspicuous basal filaments from late summer to the end of winter. We have observed the prolonged occurrence of basal remnants but no regeneration of upright filaments. Thus, we interpret it as an annual. As noted by South (1976), the size of the plant is extremely variable and it may encompass *Spongomorpha sonderi* (=*S. lanosa*) in Taylor (1962).

Spongomorpha spinescens Kützing

Common on the open coast and with scattered outer estuarine populations within the Great Bay Estuary System. Epilithic and occasionally epiphytic on coarse algae (+0.9 to −11.0m), often in tide pools. First appears in spring (April) and persists through the fall. Annual.

***Stichococcus marinus** (Wille) Hazen

Collected at two sites on the open coast (Smuttynose and White Islands) during a single date in June. Epilithic in high tide pools (+3.5m), mixed with a variety of green algae. Annual.

Stigeoclonium sp.

Found once (March) on rocks at the head-waters of the tidal limits of the Squamscott (Exeter) River (+2.0 to +2.3m). A fresh-water green alga, found mixed with *Blidingia minima* var. *subsalsa*. Annual.

Ulothrix flacca (Dillwyn) Thuret *in* Le Jolis

Common at a variety of open coastal and estuarine sites. Found on rocks, wood, metal, fucoid algae, other coarse seaweeds and halophytic flowering plants (+0.8 to +2.8m). Primarily found during the winter and spring. Annual.

Ulva lactuca Linnaeus

Abundant at a variety of open coastal and estuarine sites. Epilithic and epiphytic on coarse algae (+0.9 to −24.0m). Present throughout the year. According to Scagel (1966) and Lamb & Zimmerman (1964) the holdfast of *Ulva* may be perennial; we have not seen regeneration of the blades from the holdfast. We interpret the plant as an aseasonal annual or a pseudo-perennial.

Urospora penicilliformis (Roth) Areschoug

Common on the open coast, occasional in outer estuarine sites within the Great Bay Estuary System. Found on a wide variety of substrata (+1.2 to +2.4 m). Although it is most abundant in the winter and spring, it has been collected each month, except September. Annual.

Urospora speciosa (Carmichael *ex* Harvey in Hooker) Le Blond *ex* Hamel

Uncommon on the open coast and within the Great Bay Estuary System. Epilithic and mixed with other *Urospora* spp., *Ulothrix flacca*, and *Bangia atropurpurea* (+2.5 to +2.8m). Collected during late winter and spring. Annual.

Urospora wormskioldii (Mertens *in* Hornemann) Rosenvinge

Common on the open coast and in outer estuarine sites within the Great Bay Estuary System. Found on a variety of rocky substrata (+1.2 to +2.4m), mixed with other *Urospora* spp., *Ulothrix flacca*, *Codiolum pusillum*, *Blidingia minima* var. *minima*, *Bangia atro-*

purpurea, and various blue green algae. *In situ* populations are abundant in the winter and spring (December-May), with a few residual populations found in the summer (July). The plant was also obtained in culture from open coastal water samples (August), which were concentrated on glass fiber filters and grown in enriched seawater media (12 32 0/00) at 6 20C (R. Zechman, personal comm.). Annual.

Discussion

The chlorophycean flora of New Hampshire is characterized by a large number of annuals (82%) and a seasonally variable cycle of species numbers with a winter minimum and a summer maximum. Similar phenological patterns have been noted in other North Atlantic areas (MacFarlane & Bell, 1933; Lamb & Zimmerman, 1964; Coleman & Mathieson, 1975; Reynolds & Mathieson, 1975; Sears & Wilce, 1975), particularly sites with pronounced temperature fluctuations (cf Chapman, 1964; Williams, 1948, 1949). The phaeophycean and rhodophycean taxa within the state (Hehre & Mathieson, 1970; Mathieson & Hehre, 1982) have more pronounced seasonal cycles and greater percentages of perennial taxa than the green algae.

An evaluation of Table I suggests that there are two primary groups of chlorophycean annuals: aseasonal and seasonal. The former plants reproduce throughout the year and are represented by successive populations (see Mathieson et al., 1981), while the latter plants have a more restricted reproductive phenology. Some chlorophycean annuals (e.g. *Bryopsis plumosa*) showed a pronounced seasonal cycle of occurrence and abundance; others, such as *Monostroma oxyspermum*, were most abundant during one season (summer) and represented by residual populations at other times. Previous studies on the red and brown algae within the state (Hehre & Mathieson, 1970; Mathieson & Hehre, 1982) demonstrate a similar characterization of annuals. Detailed tagging studies of *in situ* populations would help to clarify the longevity and demography of many green algae, particularly those designated as aseasonal annuals and pseudoperennials (Knight & Parke, 1931).

As noted earlier (Fig. 3), the highest number of species were recorded on the near-shore open coast (i.e. 47 taxa). The species diversity within the Great Bay Estuary System and at the Isles of

Shoals were very similar (i.e. 46 and 42 taxa, respectively), while the lowest numbers of taxa were evident within the Hampton-Seabrook Estuary System (18 taxa). The high species diversity at the near-shore sites and the Great Bay Estuary System is probably associated with a greater variety of habitats and area than at the Isles of Shoals. Even so the Isles of Shoals represent a relatively "pristine" set of small islands with a very diverse chlorophycean flora. Overall, the near-shore open coast has a greater number of "estuarine" species than the Isles of Shoals. The species composition within the Great Bay Estuary System is very different than that at the Isles of Shoals, because of the presence of several fresh-water green algae, the enhanced number of estuarine taxa, and the reduced number of "open coastal" species (Table I). Even so, the presence of strong tidal rapids allows some "open coastal" forms to colonize estuarine areas like Dover Point (Reynolds, 1971; Reynolds & Mathieson, 1975). The differences in species diversity between the Great Bay and Hampton-Seabrook Estuary Systems may also be explained by a greater diversity of habitats, area, and substrata within the former estuary system.

In addition to the taxa listed earlier, three other green algae are recorded from the Isles of Shoals in an unpublished checklist (Anon., 1975): *Bryopsis hypnoides*?, *Rhizoclonium erectum*, and *Ulothrix laetevirens*. We have neither collected these plants nor seen voucher materials of these taxa; hence they are not included in the present synopsis.

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References

Abbott, I. A. & G. J. Hollenberg. 1976. Marine Algae of California. Stanford Univ. Press, Stanford, California. xii + 827 p.

Anonymous. 1975. Checklist of the marine flora and fauna of the Isles of Shoals. Shoals Marine Laboratory. 13 p. (mimeograph).

Blair, S. M. 1983. Taxonomic treatment of the *Chaetomorpha* and *Rhizoclonium* species (Cladophorales: Chlorophyta) in New England. Rhodora **85**: 175-211.

_____ ., A. C. Mathieson, & D. P. Cheney. 1982. Biosystematic investigations of selected species of *Chaetomorpha* (Chlorophyta: Cladophorales). Phycologia **21**: 164–172.

Chapman, V. J. 1964. The Algae. Macmillan and Company Ltd., London. viii + 427p.

Coleman, D. C. & A. C. Mathieson. 1975. Investigations of New England marine algae VII: seasonal occurrence and reproduction of marine algae near Cape Cod, Massachusetts. Rhodora **77**: 76–104.

Collins, F. S. 1912. The Green Algae of North America. Tufts College Studies, Sci. Ser. **2**: 79–480.

Daly, M. A., & A. C. Mathieson. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, U.S.A. Mar. Biol. **43**: 45–55.

De Silva, M. W. R. N., & E. M. Burrows. 1973. An experimental assessment of the status of the species *Enteromorpha intestinalis* (L.) Link and *Enteromorpha compressa* (L.) Grev. J. mar. biol. Ass. U.K. **53**: 895–904.

Dube, M. A. 1967. On the life history of *Monostroma fuscum* (Postels and Ruprecht) Wittrock. J. Phycol. **3**: 64–73.

Hanic, L. A. 1965. Life history studies on *Urospora* and *Codiolum* from southern British Columbia. Ph. D. Thesis. Univ. of British Columbia, Vancouver, B.C. 152 p.

Hehre, E. J., & A. C. Mathieson. 1970. Investigations of New England marine algae III. Composition, seasonal occurrence and reproductive periodicity of the marine Rhodophyceae in New Hampshire. Rhodora **72**: 194–239.

Hoek, C. van den. 1981. A Taxonomic Revision of the American Species of *Cladophora* (Chlorophyceae) in the North Atlantic Ocean and Their Geographic Distribution. Verh. K. Akad. Wetensch., Amsterdam, 236 p.

Jonsson, S. 1958. Sur la structure cellulaire et la reproduction de *Codiolum petrocelidis* Kuck., Algue verte unicellulaire endophyte. C. R. Acad. Sci. (Paris) **247**: 325–328.

Knight, M., & M. W. Parke. 1931. Manx Algae. Mem. Liverpool Marine Biol. Comm. **30**: 1–147.

KORNMANN, P. 1959. Die heterogene Gattung *Gomontia* I. Der sporangiale Anteil, *Codiolum polyrhizum*. Helgolander wiss. Meeresunters. **6**: 229–238.

——— ., & P. -H. SAHLING. 1977. Meeresalgen von Helgoland. Benthische Grun-, Braun- und Rotalgen. Helgolander wiss. Meeresunters. **29**:1–289.

LAMB, I. M., & M. H. ZIMMERMAN. 1964. Marine vegetation of Cape Ann, Massachusetts. Rhodora **66**: 217–254.

MACFARLANE, C., & H. P. BELL. 1933. Observations of the seasonal changes in the marine algae in the vicinity of Halifax, with particular reference to winter conditions. Proc. Nova Scotian Inst. Sci. **18**: 134-176.

MATHIESON, A. C., & R. L. BURNS. 1970. The discovery of *Halicystis ovalis* (Lyngbye) Areschoug in New England. J. Phycol. **6**: 404–405.

——— ., & E. J. HEHRE. 1982. The composition, seasonal occurrence and reproductive periodicity of the marine Phaeophyceae in New Hampshire. Rhodora **84**: 411–437.

——— ., ——— ., & N. B. REYNOLDS. 1981. Investigations of New England marine algae I. A floristic and descriptive ecological study of the marine algae of Jaffrey Point, New Hampshire. Bot. Mar. **24**: 533–545.

NIELSEN, R. 1979. Culture studies on the type species of *Acrochaete*, *Bolbocoleon* and *Entocladia* (Chaetophoraceae, Chlorophyceae). Bot. Notiser **132**: 441–449.

NIENHUIS, P. H. 1969. Enkele opmerkingen over het geslacht *Enteromorpha* Link op de schorren en slikken van Z. W. -Nederland. Overdruk uit Gorteria **4**, no. 10, pp. 178 183.

———. 1975. Biosystematics and Ecology of *Rhizoclonium riparium* (Roth) Harv. (Chlorophyceae: Cladophorales) in the Estuarine Area of Rivers Rhine, Meuse and Scheldt. Ryksuniversiteit te Groningen (Thesis). Rotterdam: Bronder Offset B. V. 240 pp.

NORRIS, J. N. 1971. Observations on the genus *Blidingia* (Chlorophyta) in California. J. Phycol. **7**: 145–149.

PRANGE, R. K. 1978. An autecological study of *Blidingia minima* var. *subsalsa* (Chlorophyceae) in the Squamish Estuary (British Columbia). Can. J. Bot. **56**: 170–179.

PRESCOTT, G. W. 1962. Algae of the Western Great Lakes Area. Revised edition. Wm. C. Brown Co. Publishers, Dubuque, Iowa, xiii + 977 p.

REYNOLDS, N. B. 1971. The ecology of a New Hampshire estuarine tidal rapid. Ph.D. Thesis. Univ. of New Hampshire, Durham, N.H., ix + 101 p.

——— ., & A. C. MATHIESON. 1975. Seasonal occurrence and ecology of marine algae in a New Hampshire tidal rapid. Rhodora **77**: 512–533.

SCAGEL, R. F. 1966. Marine algae of British Columbia and northern Washington. I. Chlorophyceae (green algae). Bull. Nat. Mus. Can. **207**: 1–257.

SEARS, J. R. 1971. Morphology, systematics and descriptive ecology of the sublittoral benthic marine algae of southern Cape Cod and adjacent islands. Ph.D. Thesis. Univ. of Massachusetts, Amherst, Mass. xiii + 295 p.

——— ., & R. T. Wilce. 1970. Reproduction and systematics of the marine algae *Derbesia* (Chlorophyceae) in New England. J. Phycol. **6**: 381–392.

——— ., & ———. 1975. Sublittoral benthic marine algae of southern Cape Cod and adjacent islands: seasonal periodicity, associations, diversity, and floristic composition. Ecol. Monogr. **45**: 337–365.

SOUTH, G. R. 1976. A check-list of marine algae of eastern Canada — First revision. J. mar. biol. Ass. U.K. **56**: 817–843.

_____ ., & R. G. HOOPER. 1980. A catalogue and atlas of the benthic marine algae of the island of Newfoundland. Memorial University of Newfoundland Occasional papers, 137 p.

TAYLOR, W. R. 1962. Marine algae of the Northeastern coast of North America. 2nd edition. Univ. of Michigan Press, Ann Arbor. ix + 509 p.

WILCE, R. T. 1970. *Cladophora pygmaea* Reinke in North America. J. Phycol. **6**: 260–263.

WILLIAMS, L. G. 1948. Seasonal alternation of marine floras at Cape Lookout, North Carolina. Am. J. Bot. **35**: 682–695.

_____. 1949. Marine algal ecology at Cape Lookout, North Carolina. Bull. Furman Univ. **31**: 1–21.

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The New England Botanical Club Council will be pleased to receive invitations to hold Club meetings at institutions in the New England area. It is expected that most of the meetings will be at Harvard, as has been the tradition, but at least two meetings will be scheduled for other Colleges or Universities each year.

TAXONOMIC IMPLICATIONS OF ANEUPLOIDY AND POLYPLOIDY IN *POTAMOGETON* (POTAMOGETONACEAE)

DONALD H. LES

ABSTRACT

A synoptic study of chromosome number reports for 73 species of *Potamogeton* presents evidence supporting the conclusion that the genus is characterized by two different polyploid lineages (one based upon $x = 7$ and the other upon $x = 13$). Analyzed comparatively, chromosome numbers also indicate that the diploid level of the genus is $2n = 14$, and that the $x = 13$ lineage arose by aneuploidy from a $2n = 14$ progenitor. Comparisons developed by juxtaposition of chromosome numbers with morphological characters and classification ranks indicate that subsections *Pusilli*, *Oxyphylli*, and *Amplifolii* may not represent entirely natural assemblages. The past use of chromosome numbers to demonstrate the primitiveness of submersed leaves in the genus is challenged due to lack of correlation of these features when a larger number of species is considered. Chromosome numbers were found to correlate geographically with the hypothetically proposed birthplace of the genus.

Potamogeton is a large (ca. 100 species) and diverse genus of strictly aquatic monocotyledons (Cook, et al., 1974). Morphological diversity in *Potamogeton* is extensive, with many of the species exhibiting heterophylly (producing both floating and submersed foliage), whereas other species possess only leaves which are entirely submersed. Researchers have often recognized two morphological groups within subgenus *Potamogeton* (*Eupotamogeton* Raunk.): the "linear-leaved" species (*e.g.*, Fernald, 1932) and the "broad-leaved" species (*e.g.*, Ogden, 1943). Both linear and broad-leaved species occur within several different subsections, thus neither group has been taxonomically well-defined. Considerably diversity within the genus is also apparent by the variety of fruit and stipule characters found among the species. *Potamogeton* is also characterized by a complex array of polyploidy which has not yet been given a thorough systematic evaluation.

While no generally acceptable classification has been developed for *Potamogeton*, taxonomists have relied for nearly 70 years upon the one developed by Hagström (1916). It has undergone only slight modifications (by St. John, 1916; Fernald, 1932; Ogden, 1943; Haynes, 1974; and others) in only portions of the genus. Hagström's classification has been criticized on several occasions for its unwieldy nature. It included 2 subgenera, 5 sections, 26 subsections,

138 species and multitudes of series, subseries, varieties, forms, and hybrids, yet neither a key to nor a synopsis of any of the ranks were given. St. John (1925, p. 462) emphasized this and stated, "There is no key of any kind. In order to identify a *Potamogeton*, it is necessary to read every page of this work, and practically memorize them." There was no critique that the ranks in the classification were not unified by a phylogenetic framework, therefore, although similar taxa were grouped together, there was little indication of overall relationships among the groups. Hagström approached classification of *Potamogeton* anatomically, largely following Raunkiaer's (1895–99) precedent. This approach was quite different from the morphologically oriented one used by Ascherson and Graebner (1907) to construct an earlier classification. Fernald (1932) later deemphasized the anatomically oriented approach, which was only to be re-emphasized again by Ogden (1943), thus resulting in ambiguity concerning which approach yielded the better classification. The classifications mentioned all predated the availability of reliable chromosomal data, hence the systematic value of chromosome number in *Potamogeton* has not been evaluated.

The first known publication of a chromosome number for any *Potamogeton* was by Wiegand (1899) for *P. foliosus*, although Palmgren (1939) erroneously cited an earlier paper by Wiegand (1898) as containing the first counts for the genus. Other early chromosome number reports for *Potamogeton* were made by Wisniewska (1931) and Kuleszanka (1934) but the first such study of any magnitude was by Palmgren (1939) and included counts for 18 species. Published counts remained relatively scarce throughout the 1940's as evidenced by Ogden's (1943) remarks. According to Goldblatt (1979), 66 species of Potamogetonaceae had published counts available, which accounted for approximately 74% of the species. Because a substantial percentage of counts for species is now available in the literature, the use of chromosome numbers to assist formulation of systematic relationships within *Potamogeton* is feasible. Additionally, replicate counts published for the same taxa assist in evaluating the credibility of a given chromosome number report.

Incorporation of chromosome counts has facilitated progress in the phylogenetic reconstruction of other genera, but this technique has not yet so been used for *Potamogeton*. Stern (1961, p. 414) stated, ". . . reported chromosome numbers indicate that a thorough

cytotaxonomic investigation of [*Potamogeton*]. . . should yield interesting results, and would be a valuable adjunct to the previous extensive morphological and anatomical studies. . ."

The purpose of this paper is to bring together chromosome number reports from the literature and to discuss them in the context of taxonomic and phylogenetic relationships within *Potamogeton*.

METHODS

A compilation of chromosome number reports published for *Potamogeton* was made from data available in the following sources: Bolkhovskikh, et al, (1969), Cave (1958–1965), Darlington & Wylie (1956), Goldblatt (1981), Löve & Löve (1974; 1975), Moore (1970–74; 1977), and Ornduff (1967 69). Morphological descriptions were located for each species for which counts were available. The descriptions were compiled from recent floristic treatments.

Synonomy is an important issue regarding how counts are best apportioned to taxa. It is recognized that the author's allocation of chromosome counts to a taxon identified as a particular species may not be in accord with some opinions. Most of the discrepancy appears to involve nomenclatural issues, however, and as such does not create a problem in terms of to which taxon a particular count should be assigned. Because of the scope of this study, however, no attempts were made to obtain verified voucher specimens which correspond with the chromosome counts reported in the literature. For the most part, synonomy presented in major floristic works was followed assuming that such works reflect the input of taxonomic expertise.

The author is also aware of controversy regarding constitution of adequate methodology for conclusively recognizing hybrids in this genus and makes no claim of possessing the ability to ascertain correctly which taxa represent hybrids and which represent "pure" species. Therefore, the decision was made to eliminate "questionable" taxa (*i.e.*, those taxa widely considered to represent sterile hybrids) from further consideration in this study.

Species names which the author accepts to represent the correct nomenclature and which are not thought to be sterile hybrids are listed in Table 1 along with the corresponding $2n$ chromosome numbers and numbers of studies corroborating each count. Names not appearing in Table 1 (and for which counts are reported) are

listed in Table 2 along with reasons for their exclusion. The morphological descriptions of the species given in Table 1 were used to construct Table 3. Morphological groups in Table 3 were delimited on the basis of the author's perspective of general morphological groups occurring in *Potamogeton*. The groups divide linear-leaved species from broad-leaved species and further separate taxa on the basis of other leaf and stipule characters. In itself, Table 3 is not meant to infer taxonomic affinities between or among taxa. The classification followed in Table 4 is that of Hagström (1916), modified only to include species described after completion of that work. The $2n$ chromosome numbers are those from Table 1. The morphological groups (A–F) are from Table 3. Fruit types, either smooth (S) or keeled (K) were designated for each species. The smooth type refers to fruits in which the dorsal keel is absent or greatly reduced, whereas the keeled fruits possess prominent dorsal keels. The assignments of fruit types were made based upon descriptions given in the following references: Aalto (1970; 1974) Komarov (1937), Ogden (1953), and Ohwi (1965). Species for which the fruit type is unknown are designated by a question mark (?).

RESULTS AND DISCUSSION

Upon examination of Table 1, six discrete ploidy levels can be detected. It is further evident that the genus is characterized by two different euploid series, one based upon $x = 7$ and the other upon $x = 13$ as previously noted by Harada (1956).

In Table 3 a correlation can be noted between chromosome numbers and the six morphological groups selected to characterize the genus. Most of the groups are dominated by one ploidy level, or at least by one of the two euploid series, which suggests a relationship between ploidy levels and general morphology of the species. Groups A and D are conspicuous exceptions because mixtures of both ploidy levels and euploid series occur. It is noteworthy that floating-leaved species occur in both of the euploid series, including the lowest levels for each (*i.e.*, $2n = 26$; 28). Furthermore, floating leaves are also produced by *P. illinoensis* which has the highest chromosome number known for any species of *Potamogeton*.

In Table 4, a comparison of species from an anatomical standpoint is given, *i.e.*, essentially the Hagström classification. Superimposed on this classification are chromosome number, morpho-

Table 1. **2*n* Chromosome numbers of *Potamogeton* species incorporated into this study**
(number of concurring references for count is given in parentheses)

Species	2*n*		Species	2*n*	
P. acutifolius	26	(2)	P. nipponicus	52	(1)
P. alpinus	52	(6)	P. nodosus	52	(3)
P. amplifolius	52	(1)	P. oblongus	26	(2)
P. asiaticus	28	(1)	P. obtusifolius	26	(1)
P. coloratus	26	(1)	P. octandrus	28	(4)
P. crispus	52	(9)	P. orientalis	28	(1)
P. cristatus	28	(2)	P. oxyphyllus	26	(1)
P. dentatus	52	(2)	P. pectinatus	78	(9)
P. distinctus	52	(2)	P. perfoliatus	52	(12)
P. epihydrus	26	(2)	P. polygonifolius	52	(2)
P. filiformis	78	(6)	P. praelongus	52	(6)
P. foliosus	28	(1)	P. pusillus	26	(6)
P. franchetti	52	(1)	P. richardsonii	52	(3)
P. friesii	26	(2)	P. robinsii	52	(1)
P. fryeri	42	(4)	P. rutilus	26	(1)
P. gramineus	52	(8)	P. sibiricus	28	(1)
P. groenlandicus	26	(1)	P. strictifolius	52	(1)
P. illinoensis	104	(2)	P. trichoides	26	(3)
P. lucens	52	(2)	P. vaginatus	78	(4)
P. maackianus	52	(2)	P. vaseyi	28	(1)
P. malaianus	52	(2)	P. zosterifolius	26	(3)
P. natans	52	(8)	P. zosteriformis	52	(1)

TOTAL: 44 species

logical group and fruit type for each listed taxon. High concordance of chromosome numbers, morphological groups and fruit types is evident in the subgenus *Coleogeton*, the section *Adnati*, and the subsections *Compressi*, *Lucentes*, *Perfoliati*, *Javanici*, and *Colorati*. Considerable heterogeneity of these features, however, is notable in subsections *Pusilli*, *Oxyphylli*, and *Amplifolii*. Species of the $x = 13$ chromosomal series possess both keeled and smooth fruits, whereas species of the $x = 7$ series have only keeled fruits (the latter type being more prevalent in the genus). More $x = 13$ species in group A

Table 2. **Disposition of problematic species having published counts**

Species	**Disposition**
P. alatus	= P. distinctus*
P. anguillanus	excluded (lack of adequate description)
P. apertus	excluded (alleged hybrid)
P. berchtholdii	= P. pusillus*
P. biwaensis	excluded (alleged hybrid)
P. compressus	= P. zosterifolius*
P. densus	excluded (= Groenlandia densa)
P. faurieri	excluded (alleged hybrid)
P. flabellatus	= P. pectinatus*
P. fluitans	exluded (alleged hybrid)
P. indicus	= P. nodosus*
P. kamogawaensis	excluded (alleged hybrid)
P. leptocephalus	excluded (alleged hybrid)
P. limosellifolius	= P. octandrus*
P. longipetiolatus	= P. distinctus*
P. malainoides	excluded (alleged hybrid)
P. miduhikimo	= P. octandrus*
P. miyakezimaensis	= P. malaianus*
P. monoginous	= P. trichoides*
P. morongii	= P. natans*
P. numsakianus	= P. octandrus*
P. panormitanus	= P. pusillus*
P. porsiaticus	excluded (lack of adequate description)
P. subfluitans	excluded (lack of adequate description)
P. subsessilifolius	= P. fryeri*
P. teganumensis	= P. dentatus*
P. tenuifolius	= P. maackianus*
P. tepperi	= P. franchetii*
P. torquatus	= P. fryeri*

TOTAL: 29 species

*Counts published under the respective problematic names were applied to these synonyms

(linear-leaved species) have smooth fruits than keeled fruits; this relationship being particularly discernible in subsection *Pusilli*. These chromosome number discrepancies indicate the need for a re-evaluation of portions of the Hagström classification.

The suggestion that morphological groups within the genus may each correlate with a different ploidy level has been made by Haynes (1974). Attempts to arrive at correlations between ploidy and morphology have led to conflicting hypotheses. An example is the question of whether species of *Potamogeton* possessing floating leaves are more primitive than their strictly submersed-leaved counterparts. Chrysler (1907, p. 183) considered the floating-leaved species to be more primitive than the submersed-leaved species, which he believed to have been derived from the former as "...a stage in the assumption of the aquatic life by the genus." He further believed that *Potamogeton* evolved from a terrestrial ancestor, the classical interpretation applied to most aquatic plants by Arber (1920), Sculthorpe (1967), and others. Cronquist (1968; 1981), however, considers *Potamogeton* to have evolved from an aquatic ancestor likely related to the dicotyledon order Nymphaeales. Haynes (1974) agreed with Cronquist and formulated a hypothesis of evolutionary progression in *Potamogeton* contradictory to the classical viewpoint. He (p. 582) invoked the "phyllode theory" (Candolle, 1827; Arber, 1920) for explaining the evolution of leaf morphology in the genus: "...one could infer that the floating leaves might have been derived from the submersed leaves by an increase in the amount of tissue between the veins near the tip of the petiole. This would imply that possibly the floating-leaved species were derived from some ancestral stock of submersed-leaved plants." Haynes supported his hypothesis with cytological data which indicated (p. 582) "The submersed-leaved species are, for the most part, diploid, whereas the floating-leaved species are, for the most part, tetraploid." His conclusion was that cytological data indicated (p. 583) "...the primitive condition probably was that of total vegetative submergence." Haynes also used chromosome numbers to support his contention that anemophily is primitive in *Potamogeton* while hydrophily is derived due to the occurrence of the latter mechanism only in species characterized by high chromosome numbers while anemophilous species were characterized by lower chromosome numbers. Although the above arguments are reasonable, there

Table 3. **Basic morphological types in Potamogeton**

I. Floating leaves absent; submersed leaves various

A. Submersed leaves linear, stipules free (Group A)

1.	P. acutifolius	(26)
2.	P. foliosus	(28)
3.	P. friesii	(26)
4.	P. groenlandicus	(26)
5.	P. obtusifolius	(26)
6.	P. orientalis	(28)
7.	P. oxyphyllus	(26)
8.	P. pusillus	(26)
9.	P. rutilus	(26)
10.	P. sibiricus	(28)
11.	P. strictifolius	(52)
12.	P. trichoides	(26)
13.	P. zosterifolius	(26)
14.	P. zosteriformis	(52)

B. Submersed leaves broad, stipules free (Group B)

1.	P. crispus	(52)
2.	P. dentatus	(52)
3.	P. lucens	(52)
4.	P. malaianus	(52)
5.	P. perfoliatus	(52)
6.	P. praelongus	(52)
7.	P. richardsonii	(52)

C. Submersed leaves linear, stipules fused (Group C)

1.	P. filiformis	(78)
2.	P. pectinatus	(78)
3.	P. robbinsii	(52)
4.	P. vaginatus	(78)

II. Floating leaves present; submersed leaves various

D. Submersed leaves linear, stipules free (Group D)

1.	P. asiaticus	(28)
2.	P. cristatus	(28)
3.	P. epihydrus	(26)
4.	P. natans	(52)
5.	P. octandrus	(28)
6.	P. vaseyi	(28)

E. Submersed leaves linear, stipules fused (Group E)

1.	P. maackianus	(52)

F. Submersed leaves broad, stipules free (Group F)

1.	P. alpinus	(52)
2.	P. amplifolius	(52)
3.	P. coloratus	(26)
4.	P. distinctus	(52)
5.	P. franchetii	(52)
6.	P. fryeri	(42)
7.	P. gramineus	(52)
8.	P. illinoensis	(104)
9.	P. nipponicus	(52)
10.	P. nodosus	(52)
11.	P. oblongus	(26)
12.	P. polygonifolius	(52)

( ) denotes $2n$ chromosome number for Table 1.

is still a discrepancy from an adaptive standpoint. If wind pollination is primitive, then why should the primitive state be characterized by total vegetative submergence, and if water-pollinated species are advanced, then why do they all lack floating leaves?

Ths Significance of Aneuploidy

Curiously, the presence of two chromosomal series within *Potamogeton* has not lead to a re-appraisal of systematic relationships among the species despite the fact it has been realized since the 1950's (Harada, 1956) and is still currently emphasized (*e.g.*, Grant, 1982). From a systematic standpoint, it would be highly desirable to know whether each line represents a monophyletic assemblage. If this indeed apears to be the case, then the classification of the genus should reflect consistent segregation of species from the separate lineages, *i.e.*, no one group should include species from both chromosomal series if a natural arrangement is to be depicted.

Investigators usually regard the euploid series based upon $x = 13$ as typical for the genus, and treat species possessing chromosome numbers of 28 or 42 as "anomalous." An example of this approach is illustrated by Haynes' (1974) treatment of subsection *Pusilli* in which he hypothesized that *P. foliosus* ($2n = 28$) was derived from a $2n = 26$ progenitor by aneuploidy. Since the other species within the subsection possess chromosome numbers based upon $x = 13$, his interpretation would appear reasonable. However, the more widespread occurrence of the $2n = 28$ species must be considered. The presence of $2n = 28$ species within the subsections *Oxyphylli* and *Javanici* (the former also including $2n = 26$ species) would imply that aneuploidy had originated independently at least two separate times in the genus, or that the subsections are not natural. All counted species within subsection *Javanici* are $2n = 28$ which implies that a single "aneuploid" event may have originated that group, but the progenitor of *Javanici* would have had to arise from a $2n = 28$ species in another subsection, or from a $2n = 26$ species by yet another aneuploid event. Furthermore, there is the questionable presence of *P. fryeri* ($2n = 42$) in a subsection characterized by $2n = 52$ species. The "anomaly" would have to be explained by still another aneuploid event in the $2n = 26$ progenitor of the group. It is unlikely, therefore, that recurring aneuploidy reasonably explains

Table 4. Relationships of chromosome numbers and morphology to sub-generic ranks (see text for explanation of symbols)

	2*n*	morphological group	fruit type
I. Subgenus: *Coleogeton*			
1. Section: *Connati*			
a. Subsection: *Filiformes*			
1. *P. filiformis*	78	C	S
2. Section: *Convoluti*			
a. Subsection: *Vaginati*			
1. *P. vaginatus*	78	C	S
b. Subsection: *Pectinati*			
1. *P. pectinatus*	78	C	S
II. Subgenus: *Potamogeton*			
1. Section: *Adnati*			
a. Subsection: *Serrulati*			
1. *P. robbinsii*	52	C	K
2. *P. maackianus*	52	E	K
2. Section: *Axillares*			
a. Subsection: *Pusilli*			
1. *P. foliosus*	28	A	K
2. *P. orientalis*	28	A	?
3. *P. obtusifolius*	26	A	S
4. *P. pusillus*	26	A	S
5. *P. friesii*	26	A	S
6. *P. rutilus*	26	A	S
7. *P. groenlandicus*	26	A	?
8. *P. strictifolius*	52	A	S
f. Subsection: *Lucentes*			
1. *P. lucens*	52	B	K
2. *P. dentatus*	52	B	K
3. *P. malaianus*	52	B	K
4. *P. distinctus*	52	F	K
5. *P. gramineus*	52	F	K
6. *P. nipponicus*	52	F	?
7. *P. illinoensis*	104	F	K
g. Subsection: *Praelongi*			
1. *P. praelongus*	52	B	K
h. Subsection: *Perfoliati*			
1. *P. perfoliatus*	52	B	S
2. *P. richardsonii*	52	B	S
i. Subsection: *Javanici*			
1. *P. asiaticus*	28	D	K
2. *P. cristatus*	28	D	K
3. *P. octandrus*	28	D	K
4. *P. vaseyi*	28	D	K
j. Subsection: *Amplifolii*			
1. *P. amplifolius*	52	F	S
2. *P. franchetii*	52	F	K
3. *P. fryeri*	42	F	K
k. Subsection: *Natantes*			
1. *P. natans*	52	D	S
l. Subsection: *Hybridi*			

b. Subsection: *Monogyni*			
1. *P. trichoides*	26	A	K
c. Subsection: *Compressi*			
1. *P. acutifolius*	26	A	K
2. *P. zosterifolius*	26	A	K
3. *P. zosteriformis*	52	A	K
d. Subsection: *Oxyphylli*			
1. *P. sibiricus*	28	A	K
2. *P. oxyphyllus*	26	A	S
e. Subsection: *Crispi*			
1. *P. crispus*	52	B	S
1. *P. epiphydrus*	26	D	K
m. Subsection: *Colorati*			
1. *P. coloratus*	26	F	S
2. *P. oblongus*	26	F	S
3. *P. polygonifolius*	52	F	S
n. Subsection: *Alpini*			
1. *P. alpinus*	52	F	K
o. Subsection: *Nodosi*			
1. *P. nodosus*	52	F	K

the origin of $2n = 28$ species. It is more likely that the $2n = 28$ species are monophyletic, have resulted from a single aneuploid event and have been simply misplaced throughout portions of the classification.

The question of the ancestral diploid number of the genus must be considered. Previous investigators (Stern, 1961; Haynes, 1974) have interpreted the chromosome numbers of $2n = 26$ or 28 to represent the diploid level in *Potamogeton*. Goldblatt (1979), however, suggested that in *Potamogetonaceae*, the base number is likely to be $x = 7$ and, therefore, all counted species of *Potamogeton* having $2n$ chromosome numbers exceeding 14 would indicate polyploidy. This interpretation is in accord with Grant (1963) and Stebbins (1971), who believe that haploid numbers in excess of $n = 10$–13 are indicative of polyploidy. The suggestion of Ehrendorfer et al. (1968) that the progenitors of the angiosperms were characterized by a base number of $x = 7$ may also be pertinent. Since *Potamogeton* is usually placed within the relatively primitive subclass Alismatidae (Cronquist, 1981; Takhtajan, 1969), it is conceivable that the base number for the genus would be $x = 7$. Evidence exists to support this interpretation. Four concurring studies have reported the chromosome number of *P. fryeri* to be $2n = 42$ (see Table 1). If $2n = 28$ is accepted as the diploid level, then *P. fryeri* would represent a triploid organism. If, however, $2n = 14$ is accepted as the diploid level, then *P. fryeri* would represent a hexaploid (while $2n = 28$ species would represent tetraploids). The latter interpretation is here accepted to be more reasonable.

Initially it was presumed that diploid ($2n = 14$) ancestors of the genus were extinct because counts of $2n = 14$ for any species of *Potamogeton* were absent from the literature. There is some indication to the contrary. A study by Wiegand (1899) reported the chromosome number of *P. foliosus* as $2n = 14$. The credibility of that report may well be questioned on the basis of whether an appropriate methodology was employed in that study. Early studies of chromosome numbers were often hampered by the use of sectioning methods (which Wiegand also used) that frequently resulted in overlooked chromosomes, but indications are that Wiegand's counts were probably accurate. It is unlikely, even by sectioning, that he would have missed half (13–14) of the chromosomes, especially since he reported the same number in his replicate counts. His illus-

trations clearly depict a chromosome number of $2n = 14$. Most convincing is the observation that Wiegand's count of $2n = 14$ is in accord with the chromosomal series to which *P. foliosus* belongs ($x = 7$). Since only two North American species are known to belong to that series, it is difficult to believe that inaccuracy on Wiegand's part would result in a count which was "coincidentally" within the proper numerical series. If the count of $2n = 14$ for *P. foliosus* is accepted as accurate, then it is evident that some species of *Potamogeton* may be characterized by different ploidy levels. As Tomlinson (1982) indicated, no cytological survey of large populations of a species has been conducted tor *Potamogeton* which could clarify this point.

The diploid level of *Potamogeton* is therefore recognized to be $2n = 14$. From this assumption follows that $x = 13$ species were derived from a $2n = 14$ diploid by descending aneuploidy. Aneuploid reduction is favored over the hypothesis of aneuploid addition to explain the patterns of chromosome number variation within *Potamogeton*. Stebbins (1966) stated that both polyploidy and aneuploid reduction are characteristic of many outcrossing species which occupy pioneer habitats. Aneuploidy is often favored in pioneer habitats since the causative unequal reciprocal translocations tie linked adaptive gene complexes (Stebbins, 1974). The genus *Potamogeton* includes outcrossing species which frequently occupy pioneer habitats.

Correlates to the Precedence of the $x = 7$ Series

The hypothesis that the $x = 7$ lineage gave rise to the $x = 13$ species of *Potamogeton* can be evaluated by how well other factors correlate with it. One factor involves the place of origin of the species. On the basis of fossil evidence, Miki (1937) suggested that *Potamogeton* originated in oriental Asia. When the geographical distributions of extant $x = 7$ species are studied, an eastern Asian affinity becomes apparent. Six of the eight known $x = 7$ species occur in eastern Asia whereas the two remaining species are found in North America (see Table 5). The $x = 7$ species are absent from other regions (with exception of the wide-ranging *P. octandrus*), and overall they represent a fairly small portion of the total number of species of *Potamogeton*. On the basis of these observations, a reasonable interpretation of evolutionary progression can be formu-

Table 5.
Geographical distributions of $x = 7$ species of *Potamogeton*

Species	$2n$	Distribution	Reference
P. asiaticus	28	Manchuria, USSR	Komarov (1937)
P. cristatus	28	China, USSR, Korea, Formosa	Ohwi (1965)
P. octandrus	28	China, USSR, Korea, Formosa, India, Malaysia	Ohwi (1965)
P. orientalis	28	Japan, eastern Asia	Hagström (1916)
P. sibiricus	28	E. Siberia (endemic)	Komarov (1937)
P. fryeri	42	Japan, Korea	Ohwi (1965)
P. vaseyi	28	United States & Canada	Hellquist & Crow (1980)
P. foliosus	28	North America	Haynes (1974)

lated. The concentration of $x = 7$ species in eastern Asia is compatible with Miki's hypothesis that *Potamogeton* originated there if this lineage is considered to be primitive. It is probable that diploid ($2n = 14$) species occurred throughout eastern Asia and that some of them dispersed into North America, which would account for the few $x = 7$ species on the latter continent. The disjunction of $x = 7$ species in eastern Asia and temperate North America coincides with the same distributional pattern of other plant species known to occur in both regions (*e.g.*, Hara, 1972). According to Raven and Axlerod (1974), the migration of plants between North America and Eurasia has been relatively unimpeded throughout much of the evolutionary history of the flowering plants, allowing migration of species across the North Atlantic region until about 49 millions years BP. When or where the $x = 13$ lineage arose is undetermined, but these species were apparently more successful than their $x = 7$ counterparts as evidenced by the larger number and wider distributions of extant $x = 13$ species. The successful radiation of $x = 13$ species throughout most continents of the world makes tracing their precise origin difficult. The relative scarcity of $x = 7$ species which survive today may be due to unsuccessful competition with their $x = 13$ descendants. Indeed, the persistence of *P. foliosus* ($2n = 28$)

in North America may be a result of the species high tolerances for various ecological extremes. In comparing the sensitivity of common aquatic plants, Stuckey (1975, p. 29) listed *P. foliosus* as an "insensitive species with wide ecological tolerances" which has "remained the same or increased in abundance through time." The greater success of $x = 13$ species is also evident from observations that this lineage includes higher level polyploids and is the only group possessing species exhibiting derived hydrophilous pollination (subgenus *Coleogeton*).

Fruit characters also reflect the ancestral nature of $x = 7$ species. Fruits of $x = 7$ species are prominently keeled (Table 4) whereas both keeled and keeless fruits occur among $x = 13$ species. The loss of keels appears restricted to the $x = 13$ lineage. Since keeled fruits occur within both chromosomal series, it is assumed that the keel represents the primitive condition. This interpretation is further supported by the occurrence of keeless fruits within subgenus *Coleogeton*. Subgenus *Coleogeton* is regarded as the most highly advanced group of the genus and the keeless fruits of the subgenus are interpreted to represent the derived state. Several species within subgenus *Potamogeton* possess fruits having small or highly reduced keels indicating a series of stages in the reduction of the structures.

Chromosome Numbers and Classification

The "working rank" in *Potamogeton* is the subsection and principal segregation of species occurs at this level. To be taxonomically meaningful, the subsections should represent monophyletic assemblages of species. An evaluation of constituent chromosome numbers is one method by which the naturalness of subsections of *Potamogeton* can be tested; however, a rationale for the analysis must be presented. In this genus, variation in chromosome number results from two processes — aneuploidy and polyploidy. As discussed above, it is probable that $x = 7$ represents the ancestral lineage. From this starting point are two possible explanations for the origin of aneuploid ($x = 13$) species. Figure 1 presents the two hypotheses. One possibility (single origin hypothesis) is that the $x = 13$ series originated by a single aneuploid event in which a $2n = 14$ diploid gave rise to a $2n = 13$ diploid which persisted by chromosomal doubling ($2n = 26$). The higher polyploids in the $x = 13$ series would have been derived from the $2n = 26$ tetraploids. In this

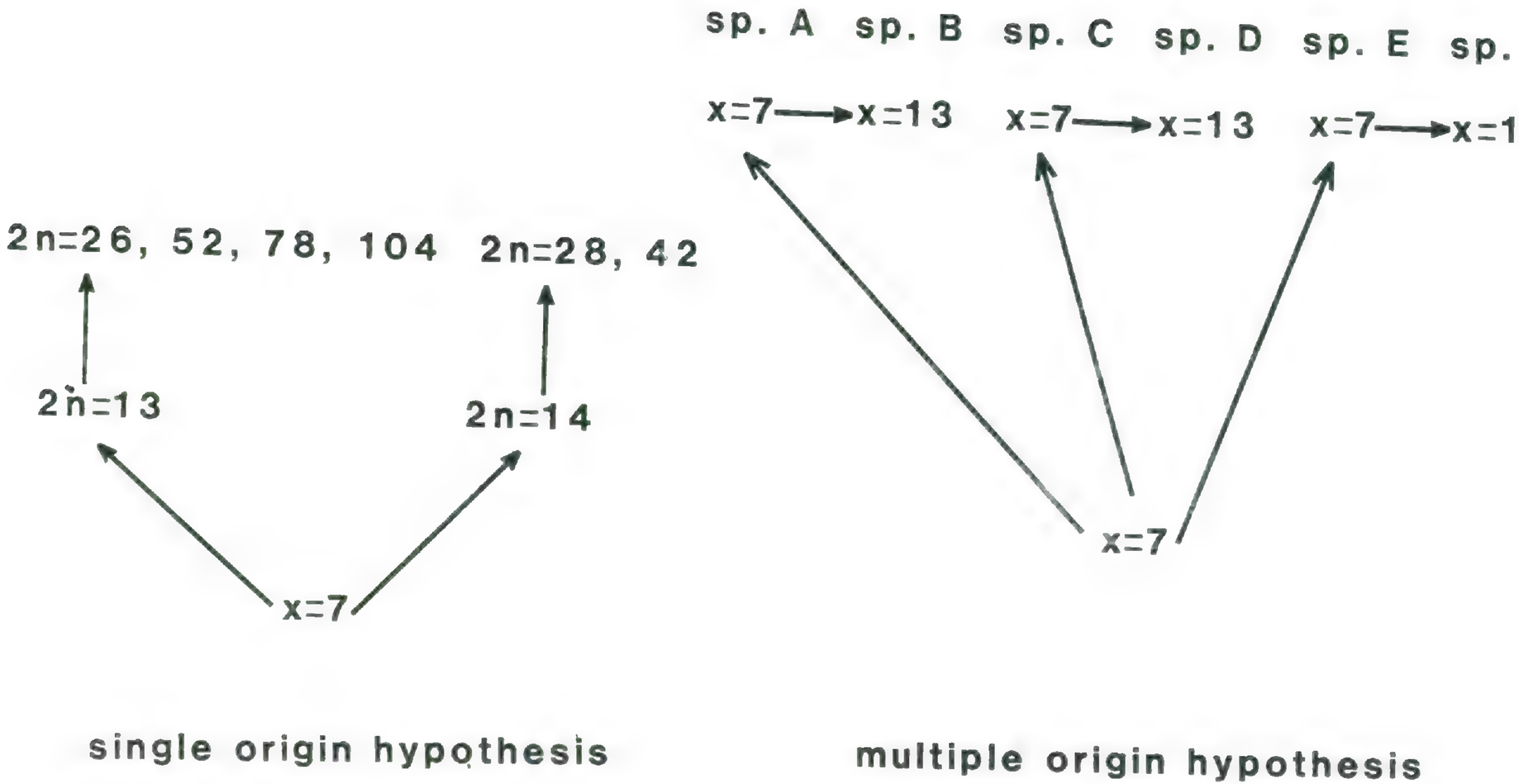

Figure 1. Hypothetical Origins of x = 13 Species

instance, the affinities between species would be greatest within the same numerical series and least between the two numerical series. In the second hypothesis, however, affinities could be much stronger between species in different series (*e.g.*, sp. A and sp. B) than between those in the same series (*e.g.*, sp. B and sp. F). If the aneuploid species arose from multiple origins, then one would expect the grouping of closely related species (such as represented by a subsection) to include members from both numerical series as well as from different ploidy levels. If aneuploid species arose from a single event, then the uniformity of subsections regarding both numerical series and ploidy levels would be expected. Referring back to Table 4, it is evident that the subsections reflect homogeneity in terms of both numerical series and ploidy levels of the constituents. This observation supports the single-origin hypothesis of aneuploid species. One difficulty in accepting this hypothesis is that subsections should be entirely characterized by species belonging to only one numerical series ($x = 7$ or $x = 13$). Although this is generally true for the representatives surveyed in this study, there are exceptions. In subsections *Pusilli, Oxyphylli* and *Amplifolii* occur species from both $x = 7$ and $x = 13$ series. This discrepancy suggests a misalignment of species. On the basis of anatomy and inflorescence characters, both subsection *Pusilli* and subsection *Oxyphylli* were noted by Hagström (1916) to be closely related to subsection *Javanici,* the only subsection comprised entirely of $x = 7$ species. It is probable, therefore, that the $x = 7$ species in subsection *Pusilli (P. foliosus* and *P. orientalis)* along with *P. sibiricus* from subsection *Oxyphylli* should rightfully be placed within or close to subsection *Javanici* instead of in their present situation. Such an adjustment would also result in a greater uniformity of fruit types within the subsections. *Potamogeton foliosus, P. orientalis* and *P. sibiricus* are also geographically related (Table 5). Likewise, the removal of *P. fryeri* from subsection *Amplifolii* may also be warranted. This species may represent a highly advanced member of subsection *Javanici* or could also be placed close to that subsection. Naturally, more detailed comparative work is needed before such taxonomic decisions can be fully justified.

With regard to polyploidy, most subsections appear to be characterized by one ploidy level, although there are a number of instances where a subsection will also include a species which is at a higher

ploidy level (*e.g.*, subsections *Pusilli, Compressi, Lucentes, Colorati*). In such situations, chromosome number alone cannot provide sufficient evidence for determining the evolutionary relationships among species. Perhaps a comparative analysis of somatic karyotypes, banding, etc., would be more revealing than simple comparisons of numbers. Because higher polyploids occur infrequently in a subsection and yet are found in various subsections, it is likely that polyploidy has occurred independently in divergent lines of $2n = 26$ species thus producing hexaploids and higher levels. In such instances, a higher level polyploid may represent an advanced member of a particular group. It is also unlikely that certain species represent transitional ploidy levels in a continuum from $2n = 26$ to $2n = 52$, 78, or 104 species, and thus could tie together phylogenetically certain subsections which are characterized by these ploidy levels. There is the question of whether a particular ploidy level (*e.g.*, $2n = 52$) has resulted from one polyploid event or from parallel polyploidy arising in divergent groups. A satisfactory elucidation of the problem may be better achieved as a result of biochemical, cytogenetic, and hybridization studies.

St. John's (1916) revision of section *Coleophylli* appeared concurrently with Hagström's (1916) monograph of *Potamogeton*. Interestingly, St. John considered *P. filiformis, P. pectinatus,* and *P. vaginatus* (as *P. moniliformis*) to belong to a single section *(Coleophylli),* whereas Hagström viewed each species as belonging to different subsections, and further divided those into two sections (*Connati* and *Convoluti*). St. John also differed from Hagström by including *P. robbinsii* in section *Coleophylli* while Hagström considered the species to belong in a different subgenus (*Potamogeton)* in section *Adnati. Potamogeton filiformis, P. pectinatus,* and *P. vaginatus* have identical chromosome numbers ($2n = 78$) which differ from that of *P. robbinsii* ($2n = 52$). *P. robbinsii* also differs from the three aforementioned species by its keeled fruit, lack of hypodermis, and presence of mechanical tissue in the peduncle (Hagström, 1916). In this respect, Hagström's inclusion of *P. robbinsii* in subgenus *Potamogeton* may be justified. On the other hand, St. John's combination of *P. filiformis, P. pectinatus* and *P. vaginatus* into one section is supported by the agreement of chromosome number, morphology and fruit type of these species.

Floating-leaved Species Primitive or Advanced?

As previously mentioned, correlations have been attempted between chromosome numbers and the presence of floating leaves. A perspective of the problem developed by examining a larger group of species fails to substantiate this correlation. The lowest representative ploidy level at which to make such a comparison is tetraploid ($2n$ = 26 or 28). At the tetraploid level, some species in each chromosomal series have floating leaves whereas others have only submersed leaves, thus presenting no clue to which morphological type arose first. Even the apparent loss of floating leaves in the advanced, high polyploid subgenus *Coleogeton* cannot be regarded as characteristic of high ploidy levels in general since floating leaves are still found at even higher ploidy levels (*e.g., P. illinoensis).* The primitiveness of floating leaves can be neither proven nor disproven solely on the basis of chromosome numbers, although other evidence may be brought to bear on the question. From an adaptive viewpoint, it is difficult to rationalize total vegetative submergence for an ancestor characterized by wind pollination. The arguments favoring an aquatic origin for *Potamogeton* have not been adequately substantiated although evidence for a terrestrial ancestry of the group is provided by Miki (1937) and den Hartog (1970). Miki believed *Potamogeton* to have originated from a different subclass (Arecidae) than is usually considered, *i.e.,* Alismatidae (Cronquist, 1981; Takhtajan, 1969), thereby destroying the "link" to the aquatic members of the Alismatidae. Den Hartog believed that marine representatives of *Potamogetonaceae* arose from terrestrial ancestors. If this is the case, then the freshwater *Potamogeton* are also likely to be of terrestrial ancestry. The more reasonable explanation still appears to be that *Potamogeton* originated with floating leaves as an intermediate stage between a terrestrial ancestry and adoption of the hydric habit. Also supporting this argument is the study by Kadono (1982) wherein the epistomatous nature of submersed and seedling leaves of several *Potamogeton* species suggested to him that submersed leaves arose from floating leaves, and that the genus possibly evolved from ancestors having floating leaves.

The appearance and disappearance of floating leaves throughout the genus is no doubt partially due to reversals. Although the genetic basis for heterophylly in *Potamogeton* is not well under-

stood, some support for this opinion exists. Heterophylly can be regulated in *P. nodosus* simply by varying the concentration of abscisic acid (Anderson, 1978) thus implying that the genetic mechanism responsible for controlling the foliar states is relatively simple. Thieret (1971) observed the production of floating leaves in *P. richardsonii* (a species that normally produces only submersed foliage) as an apparent response to dropping water levels. This changeover indicates that the genetic mechanism may still exist to produce floating leaves in species which were thought to have lost the ability to do so. Hagström (1916) apparently recognized convergence of floating-leaved species since he included both floating-leaved and submersed-leaved species within subsections on the basis of other overwhelming similarities (*e.g.*, subsections *Lucentes* and *Serrulati*).

CONCLUSIONS

A survey of chromosome numbers reported for species of *Potamogeton* has substantiated the view that the genus is characterized by two different polyploid series, one based upon $x = 7$ and the other upon $x = 13$. The diploid level of the genus is interpreted to be $2n = 14$. The $x = 13$ lineage is proposed to have arisen from one incidence of aneuploidy from a $2n = 14$ progenitor. Chromosome number data support the hypothesis that *Potamogeton* originated in Asia. A review of chromosome numbers indicates that subsections *Pusilli*, *Oxyphylli*, and *Amplifolii* may not represent entirely natural assemblages and it is suggested that a reconsideration of the classification of *Potamogeton* be made in order to accommodate discrepancies noted in regard to chromosome numbers and other features. Cytological investigations of large population samples of species are encouraged in order to obtain better insight into evolutionary processes occurring within the genus. Chromosome numbers cannot be used to directly demonstrate the primitiveness of floating leaves in the genus, although it is believed that additional evidence supports this view. Available evidence suggests a different overview of evolutionary patterns in this genus than has been previously made. Hopefully, a complete synthesis of morphological, anatomical, cytogenetic, biochemical and other data will eventually enable a more accurate phylogenetic reconstruction of *Potamogeton* to be made and thus will provide systematists with the best classification to use for this genus.

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LITERATURE CITED

AALTO, M. 1970. Potamogetonaceae fruits. I. Recent and subfossil endocarps of the Fennoscandian species. Acta Bot. Fenn. **88:** 1–85.

_____. 1974. Potamogetonaceae fruits. II. *Potamogeton robinnsii,* a seldom fruiting North American pondweed species. Ann. Bot. Fenn. **11:** 29–33.

ANDERSON, L. W. J. 1978. Abscisic acid induces formation of floating leaves in the heterophyllous aquatic angiosperm *Potamogeton nodosus.* Science **201:** 1135–1138.

ARBER, A. 1920. Water Plants: A Study of Aquatic Angiosperms. University Press, Cambridge, 436 pp.

ASCHERSON, P., & P. GRAEBNER. 1907. IV. II. Potamogetonaceae *In:* A. Engler. *Das Pflanzenreich.* Leipzig. Verlag von Wilhelm Engelmann. 184 pp.

BOLKHOVSKIKH, Z., ET AL. 1969. Chromosome Numbers of Flowering Plants [in Russian]. Acad. Sci. of the USSR, Leningrad. 926 pp.

CANDOLLE, AUGUSTE P. de. 1827. *Organographie Vegetale.* Vol. 1, book 2, chapter 3. Paris.

CAVE, M. S., ed. 1958–1965. Index to plant chromosome numbers for 1956–1964. Index for the years 1956–57 published by California Botanical Society; Index for 1958–1964 published by the University of North Carolina Press, Chapel Hill. Index to plant chromosome numbers supplement (previous to 1956) published in 1959 by California Botanical Society.

CHRYSLER, M. A. 1907. The structure and the relationships of the Potamogetonaceae and allied families. Bot. Gaz. (Crawfordsville) **44:** 161–188.

COOK, C. D. K., B. J. GUT, E. M. RIX, J. SCHNELLER, & M. SEITZ. 1974. Water Plants of the World. W. Junk b.v., publishers, The Hague, The Netherlands. 561 pp.

CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Co., Boston. 396 pp.

_____. 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York. pp. 1031–1036.

DARLINGTON, C. D., & A. P. WYLIE. 1956. Chromosome Atlas of Flowering Plants. Macmillan Co., New York. p. 337.

EHRENDORFER, F., F. KRENDL, E. HABELER, & W. SAUER. 1968. Chromosome numbers and evolution in primitive angiosperms. Taxon **17:** 337–468.

FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton* section *Axillares.* Mem. Amer. Acad. Arts. **17:** 1–183.

GOLDBLATT, P. 1979. Polyploidy in Angiosperms: Monocotyledons. *In:* W. H. Lewis, ed. Polyploidy: Biological Relevance. Plenum Press, New York. 583 pp.

_____. ed. 1981. Index to plant chromosome numbers 1975–1978. Monographs in Systematic Botany, Vol. **5.** Missouri Botanical Garden, St. Louis. 553 pp.

GRANT, V. 1963. The Origin of Adaptations. Columbia University Press, New York.

_____. 1982. Periodicities in the chromosome numbers of the angiosperms. Bot. Gaz. **143:** 379–389.

HAGSTRÖM, J. O. 1916. Critical researches on the Potamogetons. Kongl. Svenska Vetenskapsakad. Handl. **55:** 1–281.

HARA, H. 1972. Corresponding taxa in North America, Japan and the Himalayas. pp. 61–72, *In:* D. H. Valentine (ed.), Taxonomy, Phytogeography and Evolution. Academic Press, New York.

HARADA, I. 1956. Cytological studies in the Helobiae I. Chromosome idiograms and a list of chromosome numbers in seven families. Cytologia **21:** 306–328.

HARTOG, C. DEN. 1970. The Sea-grasses of the World. North-Holland Publishing Co., Amsterdam. 275 pp.

HAYNES, R. R. 1974. A revision of North American *Potamogeton* subsection *Pusilli* (Potamogetonaceae). Rhodora **76:** 564-649.

HELLQUIST, C. B., & G. E. CROW. 1980. Aquatic Vascular Plants of New England: Part 1. Zosteraceae, Potamogetonaceae, Zannichelliaceae, Najadaceae. New Hampshire Agr. Exp. Sta. Bull. **515.** 68 pp.

KADONO, Y. 1982. On the stoma found in leaves of seedlings of some *Potamogeton* species. J. Jap. Bot. **57:** 332–336.

KOMAROV, V. L., ed. 1937. Flora of the USSR (Translated from Russian in 1970 by Israel Program for Scientific Translations, Jerusalem). Vol. 1. National Science Foundation, Washington, D.C. 244 pp.

KULESZANKA, J. 1934. Rozwoz ziarn pylk u *Potamogeton fluitans*. Acta. Soc. Bot. Poloniae **11:** 457–462.

LÖVE, A. & D. LÖVE. 1974. Cytotaxonomical Atlas of the Slovenian Flora. Verlag von J. Cramer. pp. 32–36.

_____. 1975. Cytotaxonomical Atlas of the Arctic Flora. J. Cramer. In der A. R Ganter Verlag Kommanditgesellschaft. FL–9490 Vaduz. pp. 25–29.

MIKI, S. The origin of *Najas* and *Potamogeton*. Bot. Mag. **51:** 472–481.

MOORE, R. J., ed. 1970. Index to plant chromosome numbers for 1968. Regnum Veg. **68:** 16–17.

_____. 1971. Index to plant chromosome numbers for 1969. Regnum Veg. **77:** 7.

_____. 1972. Index to plant chromosome numbers for 1970. Regnum Veg. **84.**

_____. 1973. Index to plant chromosome numbers 1967–1971. Oostoek's Uitgeversmaatschappij B. V., Domstraat 5–13, Utrecht, Netherlands, pp. 47–48.

_____. 1974. Index to plant chromosome numbers for 1972. Regnum Veg. **91.**

_____. 1977. Index to plant chromosome numbers for 1973/74. Regnum Veg. **96:** 179.

OGDEN, E. C. 1943. The broad-leaved species of *Potamogeton*. Rhodora **45:** 57–105, 119–163, 171–214.

_____. 1953. Key to the North American species of *Potamogeton*. New York State Museum Circular **31,** Albany. 11 pp.

OHWI, J. 1965. Flora of Japan. Smithsonian Institution, Washington, D.C. 1067 pp.

ORNDUFF, R., ed. 1957. Index to plant chromosome numbers for 1965. Regnum Veg. **50.**

_____. 1968. Index to plant chromosome numbers for 1966. Regnum Veg. **55:** 13.
_____. 1969. Index to plant chromosome numbers for 1967. Regnum Veg. **59:** 19.
PALMGREN, O. 1939. Cytological studies in *Potamogeton*. Bot. Not. **1939:** 246–248.
RAUNKIAER, C. 1895–99. *De danske blomsterplanters naturhistorie*. Bd. I. Enkimbladede. Copenhagen. 724 pp.
RAVEN, P. H., & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. **61:** 539–673.
SCULTHORPE, C. D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London. 610 pp.
ST. JOHN, H. 1916. A revision of the North American species of *Potamogeton* of the section *Coleophylli*. Rhodora **18:** 121–138.
_____. 1925. A critical consideration of Hagström's work on *Potamogeton*. Bull. Torrey Bot. Club **52:** 461–471.
STEBBINS, G. L. 1966. Chromosomal evolution and variation. Science **153:** 1463–1469.
_____. 1971. Chromosomal Evolution in Higher Plants. Edward Arnold, London. 216 pp.
_____. 1974. Flowering Plants – Evolution Above the Species Level. Belknap Press of Harvard University Press, Cambridge. 399 pp.
STERN, K. R. 1961. Chromosome numbers in nine taxa of *Potamogeton*. Bull. Torrey Bot. Club **88:** 411–414.
STUCKEY, R. L. 1975. Submersed aquatic vascular plants as indicators of environmental quality. *In:* C. C. King and L. E. Elfner (eds.). Organisms and biological communities as indicators of environmental quality –a symposium. Ohio Biological Survey Informative Circular No. **8.** pp. 27–30.
TAKHTAJAN, A. 1969. Flowering Plants –Origin and Dispersal. Oliver and Boyd: Edinburgh. 310 pp.
THIERET, J. W. 1971. Observations on some aquatic plants in northwestern Minnesota. Michigan Bot. **10:** 117–124.
TOMLINSON, P. B. 1982. VII. Helobiae (Alismatidae) (including the seagrasses). *In:* C. R. Metcalfe, ed. Anatomy of the monocotyledons. Clarendon Press, Oxford. 522 pp.
WIEGAND, K. M. 1898. Notes on the embryology of *Potamogeton*. *In:* W. F. Ganong "Society for Plant Morphology and Physiology" report of the Ithaca meeting, December 28–29, 1897. Bot. Gaz. **25:** 116.
_____. 1899. The development of the microsporangium and microspores in *Convallaria* and *Potamogeton*. Bot. Gaz. **28:** 328–359.
WISNIEWSKA, E. 1931. Rozwoz ziarn pylku u *Potamogeton perfoliatus* L. Acta. Soc. Bot. Poloniae **8:** 157–174.

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DISTRIBUTION OF *PODOSTEMUM CERATOPHYLLUM* MICHX. (PODOSTEMACEAE)[1]

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ABSTRACT

Podostemum ceratophyllum is an often overlooked freshwater dicot, restricted to areas of swift moving river currents—an apparently ecologically sensitive habitat. Selected specimens representing the entire range of the plant are listed.

Podostemum ceratophyllum (Riverweed), a freshwater aquatic dicot, grows attached to rocks in river rapids and waterfalls. The plant tends to be undercollected because of its often inaccessible habitat and inconspicuous appearance (often mistaken for an aquatic moss or freshwater alga) (Philbrick, 1981, 1982). Consequently, its current distribution is unclear. The purpose of this paper is to provide a distributional record of *P. ceratophyllum* based on specimens from 41 herbaria.

Podostemum ceratophyllum is the single North American member of an otherwise tropical family, Podostemaceae. *Podostemum ceratophyllum* exhibits the widest distribution of any species in the genus, ranging from central Nova Scotia, central New Brunswick and southern Quebec, southward along the eastern United States to Georgia, and westward to Kentucky and eastern Oklahoma (Fig. 1). Raymond (1950) reports a location in eastern Wisconsin but we have not seen a specimen that documents this site. The species is also represented in the West Indies (Dominican Republic) and in Central America (Honduras, as var. *circumvallatum*), although very few specimens document this southernmost portion of its range. The remaining 16 or so species in the genus occur in the southern hemisphere from southern Brazil south to Argentina and Paraguay (Royen, 1954). There are also species reported from Africa and India, but their position in this genus is uncertain (Graham & Wood, 1975; Royen, 1954; Willis, 1902).

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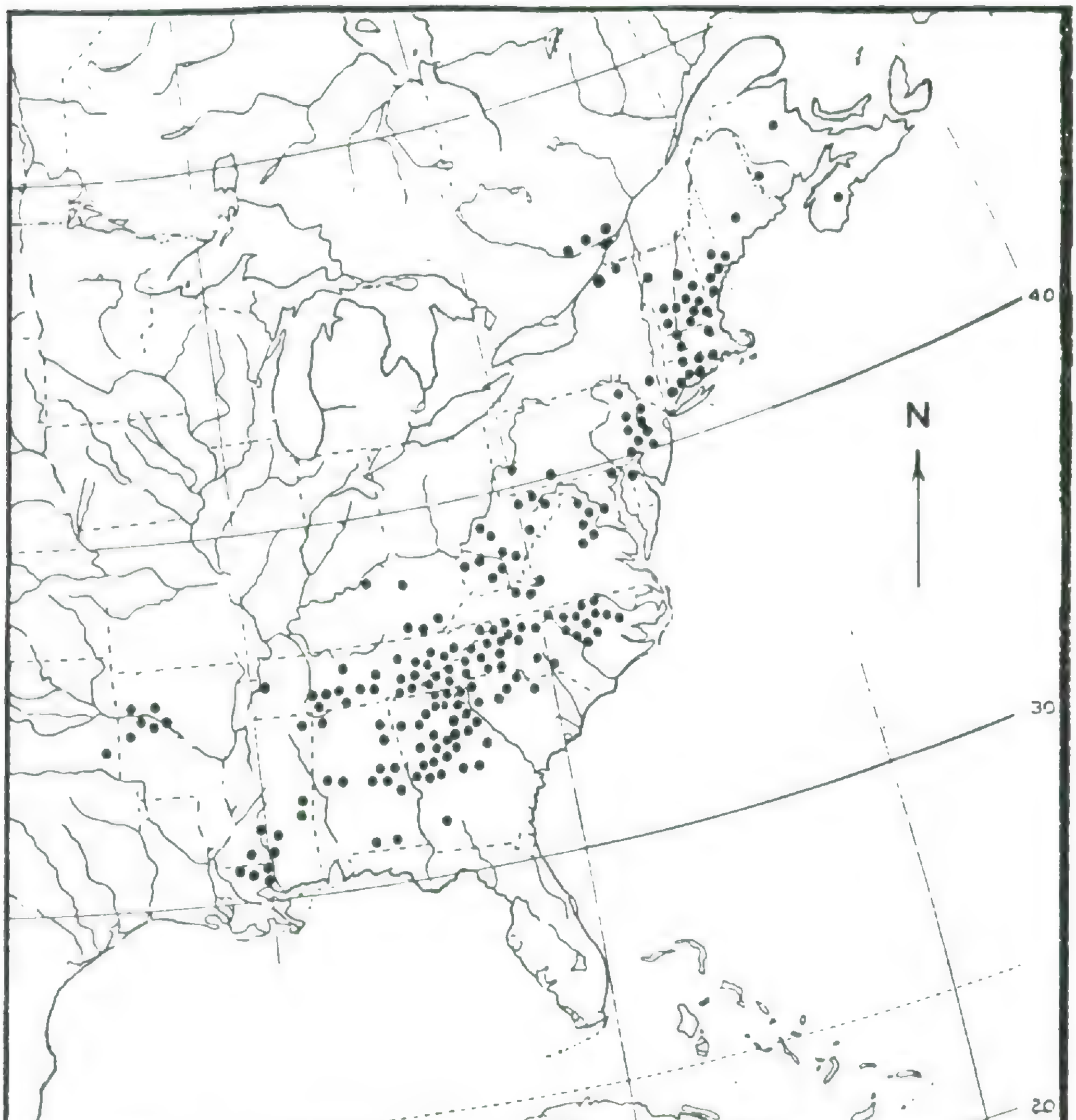

Figure 1. Distribution of *Podostemum ceratophyllum*.

The lack of documentation of *Podostemum ceratophyllum* was briefly discussed by Muenscher and Maguire (1931) for New York. It has recently been accessed as rare in New England (Crow et al., 1981). However, during the summer of 1981 numerous previously unknown stations for the plant were documented in southern New Hampshire and southern Maine (Philbrick, 1982). This suggests that the plant is much more common in this region than previously believed. On the other hand, while many locations for *Podostemum* have been documented in New England since the late 1800's, several of the earlier known stations no longer harbour the plant. The plant has not been collected from the first known New England station (Killingworth, Conn.) since 1925, and Countryman (1978) reported its absence at Jamaica, the earliest known Vermont site. Recent searches of Rhode Island stations were unsuccessful in finding the plant.

In many respects the habitat of *Podostemum ceratophyllum* is ecologically harsh, as illustrated by the fact that there are virtually no angiosperms with which *Podostemum* must compete for growing space. Several species of *Potamogeton,* however, occasionally grow in the gravel between the rocks on which *Podostemum* is attached. This habitat also seems ecologically sensitive. Any manipulation of this environment resulting in substratum modification, water flow changes, or deterioration of water quality could result in the death of the plant. Drastic changes in water flow seem to be the most obvious cause of extirpation of the plant. Countryman (1978) reports that the West River population at Jamaica, Vermont, seems to have been extirpated due to river flow manipulation. It is also believed that one of the two documented New Brunswick, Canada, locations is currently inundated to a depth that prevents growth (H. Hinds, pers. comm).

Water pollution and siltation may also have drastic negative effects on *P. ceratophyllum*. Such factors may have resulted in its loss from a location in the Cocheco River at Dover, New Hampshire. Although numerous specimens document the site, we could not locate any plants during 1980–1982. Its apparent disappearance may be related to a mass fish-kill in the Cocheco River. This fish-kill is reported to have been linked to industrial waste dumping in July of 1973, several miles upstream from the *Podostemum* population (Thayer, 1973, unpublished).

Although *Podostemum* is, no doubt, sensitive to specific pollutants, all pollutants are not detrimental to the species. The first author has collected the plant from the Mousam River, Kennebunk, Maine, where the river is noticeably polluted by domestic sewage. The Winooski River in South Burlington, Vermont, is also polluted (W. Countryman, pers. comm.) but the plant grows well. It is therefore apparent that the plant is not as good an indicator of clean water as Meijer (1976) proposed.

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LITERATURE CITED

Countryman, W. D. 1978. Rare and Endangered Vascular Plants Species of Vermont. The New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service [Newton Corner, MA].

Crow, G. E., W. D. Countryman, G. L. Church, L. M. Eastman, C. B. Hellquist, L. J. Mehrhoff, & I. M. Storks. 1981. Rare and endangered vascular plant species of New England. Rhodora **83**: 259–299.

Graham, S. A., & C. E. Wood, Jr. 1975. The Podostemaceae of the southeastern United States. J. Arn. Arb. **56**: 456–465.

Meijer, W. 1976. A note of *Podostemum ceratophyllum* Michx. as an indicator of clean streams in and around the Appalachian Mountains. Castanea **41**: 319–324.

Muenscher, W. C., & B. Maguire. 1931. Notes on some New York plants. Rhodora **33**: 165–167.

Philbrick, C. T. 1981. Some notes regarding pollination in a New Hampshire population of *Podostemum ceratophyllum* Michx. (Podostemaceae). Rhodora **83**: 319–321.

———. 1982. New locations for *Podostemum ceratophyllum* Michx. (Podostemaceae) in New Hampshire and Maine, with some comments on a unique floral form. Rhodora **84**: 301–303.

Raymond, M. 1950. Esquisse phytogeographique du Quebec. Mem. Jarb. Bot. Montreal **5**: 1–447.

Royen, P. van. 1954. The Podostemaceae of the New World. Part III. Act. Bot. Neerl. **3**: 215–263.

THAYER, T. A. 1973. The Cocheco River, its Composition and Effect on the Community. (xeroxed report). University of New Hampshire, Durham.
WILLIS, J. C. 1902. A revision of the Podostemaceae of India and Ceylon. Ann. Roy. Bot. Gard. (Peraedeniya) **1**: 181–465.

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APPENDIX: REPRESENTATIVE SPECIMENS

The following locality information is based on specimens from ACAD, APSU, CM, CLEMS, CONN, DUKE, F, FLAS, GA, GH, HNH, LAF, MAINE, MASS, MICH, MIN, MO, NCSC, NCU, NEBC, NHA, NLU, NO, NSPM, NY, OS, OKLA, PH, SMU, TENN, UARK, UNA, US, USF, VDB, VPI, VT, WIS, WVA, Tennessee Valley Authority collection (TVA), and Western Kentucky University (WKU). For simplicity most fractional units have been changed to decimal.

CANADA. NEW BRUNSWICK. **Northumberland Co.:** Quarryville, *Webster and Fielding 225* (1955) (ACAD, NSPM); near Woodstock, Eel River, *Macoun 22593* (1899) (CA, F). NOVA SCOTIA. **Lunenburg Co.:** LaHave River, *Wilson and Wright, s.n.* (1982) (NHA, NSPM).

ONTARIO. **Hastings Co.:** Actinolite, Skoutamata River, *Catling, s.n.* (1977) (OS); vicinity of Ottawa, Brighams Creek, *Macoun 5907* (1898) (F).

QUEBEC. **Argenteuil Co.:** opposite Hawkesburg, *Dore 18641* (1960) (LAF, NHA). **Deuxmontagnes Co.:** Ile Yale, Mille Iles River, *Marie-Victorin, Gervais and Lavigne, s.n.* (1969) (US); Ile Bizard, *Marie-Victorin 22081* (1925) (MO, WIS, PH, MIN, F. ACAD); St. Eustache, *Victorin 3212* (1916) (MO, NY, US). **Gatineau Co.:** Hull, *Macoun, s.n.* (1894) (MO, MICH, NY, MIN); Hull, Ottawa River, *Moyle, s.n.* (1959) (MIN). **Vaudreuil Co.:** Ile Perrot, *Cody and Dore 6565* (1952) (PH, MAINE, WIS, MICH, US, NY); Ile Des Pins, Vaudreuil, *Marie-Victorin, s.n.* (1960) (US).

UNITED STATES. ALABAMA. **Bibb Co.:** SW of West Blockton, Little Cahaba River, *Haynes 7462* (1979) (UNA). **Cherokee Co.:** Centre, Terrapin Creek, *Kral 31759* (1968) (OS, SMU, VDB); Ellisville,

Terrapin Creek, *Haynes 7329* (1979) (UNA). **Clay Co.:** Lineville, Crooked Creek, *Haynes 7372* (1979) (UNA, VDB). **Coosa Co.:** SW of Rockford, Swamp Creek, *Haynes 7904* (1980) (UNA). **Covington Co.:** "the shoals", Patsaliga Creek, *Harper 106* (1906) (GH, MO, NY, US). **De Kalb Co.:** Little River, *Wiersema 376* (1978) (UNA); NW of Gaylesville, Little River, *Haynes 6587* (1978) (UNA); 1 mi. W of junction with Little River, Hicks Creek, *Clark and Landers 5101* (1966) (NCU); Lake Guntersville State Park, Town Creek, *Meigs 930* (1980) (UNA). **Geneva Co.:** 5 mi. SW of Coffee Springs, Double Bridges Creek, *McDaniel 8566* (1967) (VDB). **Lauderdale Co.:** Florence, Cypress Creek, *Snoddy, s.n.* (1978) (TVA); N of Florence, Little Cypress Creek, *Haynes 6784* (1978) (UNA, VDB); Pruitton, Butler Creek, *Harper 3870* (1942) (F, GH, PH, US, WIS); Mussell Shoals, Tennessee River, *Harper, s.n.* (1922) (NY, PH, US). **Lee Co.:** near Bean's Mill, Halawakee Creek, *Wiersema 831* (1979) (UNA); Chewacla State Park, Chewacla Creek, *Johnson 51* (1959) (NCU); Wright's Mill, Little Uchee Creek, *Haynes 7858* (1980) (UNA). **Marshall Co.:** 4.5 mi. SSE of Lake Guntersville State Park, Short Creek, *Webb 3005* (1980) (TVA). **Randolph Co.:** Wadly, Tallapoosa River, *Haynes 7354* (1979) (UNA). **Tallapoosa Co.:** N of Reeltown, Songahatchee Creek, *Haynes 7879* (1980) (UNA); Samantha, North River, *Davenport 1204* (1979) (UNA, VDB); Alexander City, Elkahatchie Creek, *Kral 43308* (1971) (VDB).

ARKANSAS. **Conway Co.:** Petit Jean State Park, Cedar Creek, *Morrilton 722* (1955) (TENN, UARK). **Franklin Co.:** Taft, Mulberry Creek, *Moore, s.n.* (1952) (UARK). **Montgomery Co.:** Caddo Gap, Caddo River, *Moore 54-111* (1954) (F, TENN, UARK, WIS); Pine Ridge, Ouachita River, *Harris, Basco and Douglas, s.n.* (1977) (NLU). **Pope Co.:** Ozark National Forest, Big Pingy Creek, *Hamilton 41* (1969) (NCU); Dover, Twin Bridges, *Tucker 5791* (1967) (NCU); Cossatut Creek, *Moore 510673* (1951) (UARK). **Van Buren Co.:** Shirley, Little Red River, *Clark 92b* (1971) (UARK).

CONNECTICUT. **Fairfield Co.:** Bridgeport, Pequomock River, *Eames 9519* (1917) (CONN, NEBC); Fairfield, Mill River, *Eames and Godfrey 5296* (1906) (CONN, MIN); Huntington, Farmill River, *Eames 5290* (1905) (CONN, MIN); Newtown, *Nichols, s.n.* (1979) (NEBC); Trumbull, Pequonnock River, *Eames 11722* (1935) (CONN, GH). **Hartford Co.:** Windsor, "Rainbow", *Clark, s.n.* (1904) (CONN). **Middlesex Co.:** Killingworth, [Hammonasset River], *Hall, s.n.*

(1874) (CONN, NEBC); East Haddam, Devil's Hopyard, *Eames, s.n.* (1933) (CONN). **New Haven Co.:** Oxford, Little River, *Harger 2356* (1902) (CONN, GH). **Tolland Co.:** Mansfield, Mt. Hope River, *Macgregor and Torrey 4391* (1948) (CONN (2)); Mansfield, Willimantic River, *Torrey 4410* (1948) (CONN (3)). **Windham Co.:** South Chaplin, Natchaug River, *Heisey, s.n.* (1974) (CONN); Canterbury, Little River, *Goldstein 101* (1974) (CONN).

DELAWARE. **New Castle Co.:** Wilmington, Brandywine Creek, *Canby, s.n.* (1883) (MASS); Faukland, Red Clay Creek, *Commons, s.n.* (1886) (CM, USF); Greenbank, Red Clay Creek, *Commons, s.n.* (1884) (MO, NY (2), PH US).

GEORGIA. **Cherokee Co.:** SW of Canton near Cherokee Mills, Little River, *Duncan 8336* (1948) (GA). **Clarke Co.:** SW of Athens, Bobbin Mill Creek, *Pyron and McVaugh 78* (1935) (NO); Tallassee Shoals, *Pyron, s.n.* (1935) (CLEMS, GA). **Dawson Co.:** Dawsonville, Amicalola Creek, *Pyron and McVaugh 1006* (1936) (GA). **Dougherty Co.:** Albany, Flint River, *Chapman, s.n.* (unknown date) (NY); Muckafoonee Creek, *Harper 1950* (1903) (F, GH, MO, NY, US). **Elbert Co.:** NW of Elberton, Broad River, *Duncan 11714* (1950) (GA, GH, NCSC); Ga. Highway 172, Broad River, *Coile and Bates 1994* (1978) (FLAS, NCU). **Floyd Co.:** Rome, Coosa River, *Chapman, s.n.* (1937) (F, MO, US). **Fulton Co.:** SE of Roswell, Chattahoochee River, *Duncan and Venard 16522* (1953) (GA, NCSC); NW of Norcross, Chattahoochee River, *Welch, s.n.* (1965) (CM, GA). **Gilmer Co.:** Doll Mountain public access area, Coosawattee River, *Kral 50866* (1973) (VDB). **Gwinnett Co.:** 1 mi. below Old Jones Bridge, Norcross, *Huisch, s.n.* (1964) (GA). **Habersham Co.:** Soque River, *Nee, Peet and Arnold 1748* (1969) (WIS); S of Clayton, Tallulah River Gorge, *Michener 1430* (1975) (NCU). **Harris Co.:** N of Fortson, *Duncan 9248b* (1949) (GA); Robert Lewis Scout Camp, Mulberry Creek, *Jones 21868* (1972) (NCU). **Hart Co.:** NW of Hartwell, Shoal Creek, *Duncan 7821* (1947) (GA). **Jones Co.:** E of James, Altamaha River, *Suttkus 2518* (1955) (MO, NO); Highway 22, Commissoner Creek, *Musselman 4402* (1972) (NCU). **Madison Co.:** S of Carlton, Andrew's Shoals, south fork of Broad River, *Scott, s.n.* (unknown date) (GA, GH, MO); Comer, *Pyron, s.n.* (1934) (DUKE). **Madison-Oglethorpe Co. Line:** S of Carlton, south fork of Broad River, *Suttkus, s.n.* (1953) (DUKE, NCU (2), NO, NLU). **McDuffie Co.:** Rt. 79, Little River, *Leeds, s.n.* (1933) (PH). **Meriwether Co.:** Flat Shoals,

Flint River, *W.A.J. and B.B.H., s.n.* (1938) (GA, LAF, NCU, NLU, WVA). **Morgan Co.:** Farmington, Double Shoals, Appalachia River, *Jones 21012* (1971) (GA). **Newton Co.:** Covington, Bear Creek, *Rogers, s.n.* (1963) (GA). **Oglethorpe Co.:** Lexington, Echols Mill, *Montgomery 933* (1967) (DUKE, F, FLAS, GA, LAF, MASS, MO, NCU, NCSC, NLU, NO, NY (2), PH, TENN, UNA (2), USF, VDB, WVA); Comer, south Broad River, *Pyron and McVaugh 41* (1935) (DUKE, F, GH, MO, PH (2)); Carlton, Andrew's Mill, south fork Broad River, *Duncan 11647* (1950) (DUKE, FLAS, GH, MICH, MIN (2), MO, NCSC, SMU, TENN, UNA, US). **Pike-Meriwether Co. Line:** W of Concord, Flint River, *Pyron and McVaugh 1831* (1937) (GA). **Rabun Co.:** base of Big Mountain, Chattooga River, *DuMond 1189* (1968) (NCSC, WKU); WSW of town of Pine Mountain, *Sutkus 2531* (1955) (GA, LAF, NO). **Rockdale Co.:** Logansville, Haynes Creek, *Pyron and McVaugh 552* (1936) (MICH, US). **Stevens Co.:** 1 mi. upstream from confluence with Tugaloo River, Panther Creek, *Boufford, Massey and Katz 16988* (1975) (NCU); N of Toccoa, Cedar Creek, *Boufford and Wood 16799* (1976) (NCU); S of Toccoa, Broad River, *Scott 91* (1949) (GA). **Talbot Co.:** ENE of Manchester, Flint River, *Jones 21098* (1971) (GA). **Towns Co.:** W of Hiawassee, Hiawassee River, *Wherry and Pennell 14075* (1927) (PH); Hiawassee, Center Creek, *Scott, s.n.* (unknown date) (GA). **Upson Co.:** 3 mi. W of Thomaston, Potatoe Creek, *McVaugh 8939* (1948) (MICH, MO, NLU, NCU, SMU, VDB); SE of Woodbury, Flint River Gorge of Pine Mountain, *Jones and Faust 22036* (1972) (DUKE, GA). **Walton Co.:** Athens, Apalachee River, *Pyron and McVaugh 66* (1935) (GA). **White Co.:** E of Helen, *Duncan 20778* (1958) (GA).

KENTUCKY. **Fayette Co.:** Kentucky River, *Peter, s.n.* (1833) (MICH, MASS). **Harlan Co.:** near Harlan Court House, *Kearney 19* (1893) (GH, MIN, US). **Jefferson Co.:** Falls of Ohio River, *Short, s.n.* ("1840") (NY (3), PH). **McCreary Co.:** Tennessee-Kentucky Line, big south fork of Cumberland River, *Wofford 78-99* (1978) (TENN). **Menifee-Wolfe Co. Line:** E of Gladie Creek, Red River, *Meijer, s.n.* (1974) (WKU). **Whitley Co.:** Cumberland Falls, Cumberland River, *McFarland 95* (1940) (DUKE, GA, GH, MICH, MIN (2), MO, NHA, NY, PH, TENN, US, WVA). **Whitley-McCreary Co. Line:** Cumberland Falls, *Braun 2633* (1939) (US, WIS).

LOUISIANA. **St. Helena Parish:** NE of Montpelier, Tickfaw River, *Allen 1923* (1972) (LSU). **St. Tammany Parish:** NW of Covington,

Bogue Falaya, *Thieret 27013* (1967) (DUKE, GH, LAF, VDB). **Tangipahoa Parish:** Amite River, *Cooley and Brass 4183* (1955) (USF); E of Independence, Tangipahoa River, *Thomas 40377* (1974) (CM, FLAS, GA, MASS, MO, NCU, NLU, PH). **Washington Parish:** W of Warnerton, Pearl River, *Suttkus 2770* (1959) (NO); SW of Franklinton, Bogue Chitto River, *Thieret 29307* (1968) (DUKE, FLAS, GA, NCU, SMU).

MARYLAND. **Baltimore Co.:** unknown locality, *Shreve, s.n.* (1902) (MIN). **Cecil Co.:** ESE of Pilot, Conowingo Creek, *Wilkens 6855* (1941) (NCU, PH). **Garrett Co.:** Deep Creek, *Drouet 2346* (1938) (F); Swallow Falls State Forest, Muddy Creek, 8 mi. NNW of Oakland, *Herman 14915* (1958) (US); Savage Station, *Williamson, s.n.* (1905) (PH (3)). **Howard Co.:** Savage Station, Patuxent River, *House 1521* (1905) (MO). **Prince Georges Co.:** NW of Bowie, Patuxent River, *Hermann 9940* (1938) (F, NY).

MAINE. **Cumberland Co.:** Yarmouth, Royal River, *Philbrick 1136* (1981) (NHA). **Cumberland-Sagadahoc Co. Line:** Brunswick-Topsham line, Androscoggin River, *Philbrick 1135* (1981) (NHA). **Kennebec Co.:** Benton Village, Sebasticook River, *Rossbach 4965* (1959) (MAINE, NCU); Clinton, Sebasticook River, *Rossbach 5029* (1959) (MAINE (4), NCU); West Gardiner, Collin's Dam, *Fassett 18295* (1936) (F, GH, MAINE, MIN, MO, NEBC, NY). **Lincoln Co.:** Alna, Sheepscott River, *Philbrick 1113* (1981) (NHA); Cooper's Mills, Sheepscott River, *Philbrick 1117* (1981) (NHA); Whitefield, Sheepscott River, *Philbrick 1115* (1981) (NHA). **Penobscot Co.:** Alton, Pushaw Stream, *Steinmetz 1188* (1942) (MAINE); Bradley, Chemo Stream, *Merrill 861* (1898) (US); Old Town, Gilman Falls, *Steinmetz and Ogden 840* (1937) (CONN, F, GH, MAINE, MASS, MICH, MO, NCSC, NCU (2), NEBC, NY, OKLA, PH (2), SMU, US, VT, WIS, WVA); Old Town, Gilman Falls, *Bicknell, s.n.* (1952) (MAINE); Orono, Pushaw Stream and Stillwater River, *Steinmetz, s.n.* (1939) (PH, (2)). **York Co.:** Kennebunk, Mousam River, *Philbrick 1137* (1981) (NHA); Sanford, Mousam River, *Philbrick 1142* (1981) (NHA).

MASSACHUSETTS. **Franklin Co.:** Deerfield, *Poland, s.n.* (1959) (MO). **Hampshire Co.:** Amherst, Connecticut River, *Jesup, s.n.* (unknown date) (NHA); Belchertown, Jabish Brook, *Thies, Thies, Thies and Seymour 5521* (1940) (WIS (2)); Mt. Holyoke, Connecticut River, *Jesup, s.n.* (1874) (MASS, HNH); South Hadley, Stony Brook, *Ahles 84604* (1977) (MASS); Southhampton, unknown collector, *s.n.* (unknown date) (MO). **Middlesex Co.:** South Natick, Charles River,

Faxon, s.n. (1883) (GH, MASS, MIN, NEBC (2), US); South Natick, Charles River, *Philbrick 1124* (1981) (NHA).

MISSISSIPPI. **Clarke Co.:** 2 mi. N of Enterprise, Chunky River, Dunn's Fall, *McDaniel 23005* (1979) (NO, VDB, TENN). **Covington Co.:** N of Sumrall, Bowie River, *Barnes 658* (1976) (VDB). **Lauderdale Co.:** E of Chunky, Chunky River, *McDaniel and Clark 14602* (1970) (GA). **Marion Co.:** E of Sandy Hook, Pearl River, *Suttkus 2537* (1955) (NO). **Pike Co.:** between Pricodale and Hulmerville, Topisaw Creek, *Robers 7916* (1972) (NCU, NLU, TENN, USF, VDB). **Simpson Co.:** 8 mi. SW of Pinola, Strong River, *Wallus, s.n.* (1971) (FLAS, NLU, USF). **Tishomingo Co.:** Tishomingo State Park, Bear Creek, *Pollen 65351* (1965) (NCU); Bear Creek, *Rogers 45866* (1978) (TENN).

NEW HAMPSHIRE. **Belknap Co.:** Barnstead, Suncook River, *Krochmal 1496* (1948) (NHA). **Carroll Co.:** Effingham-Freedom line, Ossippee River, *Philbrick 1134* (1981) (NHA). **Coos Co.:** N of Lancaster, "Pothole", *Krochmal 1420* (1948) (NHA). **Hillsboro Co.:** Antrim, North Branch Brook, *Krochmal and Dole 1040* (1947) (NEBC, NHA); Hillsboro, Beard's Brook, *Krochmal and Dole 1015* (1947) (NHA); Hillsborough, Beard's Brook, *Philbrick 1099* (1981) (NHA). **Merrimack Co.:** Boscawen, Contoocook River, *Philbrick 1100* (1981) (NHA); Henniker, Contoocook River, *Philbrick 1150* (1981) (NHA); Hopkington, Contoocook River, *Philbrick 1152* (1981) (NHA). **Rockingham Co.:** Epping, Lamprey River, *Philbrick 1111* (1981) (NHA); Raymond, Lamprey River, *Philbrick 1109* (1981) (NHA). **Strafford Co.:** Barrington, Isinglass River, *Philbrick 1119* (1981) (NHA); Dover, Witcher's Falls, Cocheco River, *Hodgdon 19546* (1972) (MASS, NHA); Dover, Witcher's Falls, Cocheco River, *Hellquist 2029* (1973) (WVA); Durham, Packer's Falls, Lamprey River, *Philbrick 1102* (1981) (NHA). **Sullivan Co.:** Plainfield, Connecticut River, *Zika 4433* (1981) (VT).

NEW JERSEY. **Cape May Co.:** Bennett, *Stone 15713* (1917) (PH); Stockton, *Fisher, s.n.* (1895) (PH). **Hunterdon Co.:** 2 mi. above Wallpack Bend, Delaware River, *Edwards, s.n.* (1947) (NY); Princeton, Pretty Brook, unknown collector, s.n. (unknown date) (NY); near Phillipsburg, Delaware River, *Porter, s.n.* (1870) (US). **Sussex Co.:** opposite Bushkill, Delaware River, *Bartram, s.n.* (1917) (PH). **Warren Co.:** Foul River, *Van Pelt, s.n.* (1907) (PH); Marble Hill, Delaware River, *Porter 1379* (1869) (PH).

NEW YORK. **Franklin Co.:** Hogansburg, St. Regis River, *Muenscher, Bassett and Maguire 1197* (1930) (F, MIN, MO, US, WIS). **St. Lawrence Co.:** rapids below Messena, Grasse River, *Muenscher, Bassett and Maguire 1198* (1930) (F, GH, HNH, MIN, MO, US, WIS); Hogansburg, St. Regis River, *Muenscher and Justice 839* (1938) (CONN, F, FLAS, MAINE, MASS, MICH, MIN, MO, NCSC, NCU (2), NHA, NY, OKLA, PH (2), US, VT). **Ulster Co.:** Glenerie Falls, *Wilson, s.n.* (1916) (NY (3)); Shawangunk Kill, *Wilson, s.n.* (1922) (NY).

NORTH CAROLINA. **Alexander Co.:** 7 mi. SW of Taylorsville, Middle Little River, *Radford 18147* (1956) (NCU); Millersville, Glade Creek, *Beal* 5870 (1960) (NCSC). **Alleghany Co.:** 1.6 mi. N of Amelia, New River, *Radford 44194* (1961) (MASS, NCU, UARK, UNA, WIS). **Ash Co.:** 2 mi. SE of Scottsville, Cranberry Creek, *Beal 6064* (1961) (NCSC). **Avery Co.:** 3.4 mi. E of Grandmother Gap, Wilson Creek, *Ahles and Duke 49578* (1958) (NCU). **Buncombe Co.:** at Batcave, near Rt. 9, Flat Crick Falls, *Radford 4867* (1949) (NCU). **Burke Co.:** High Shoals, *Smith 305* (1975) (NCSC). **Caldwell Co.:** stream at Colletsville *Radford and Radford 6251* (1952) (GH, NCU); N of Patterson, Buffalo Creek, *Beal 7126* (1961) (NCSC). **Chatham Co.:** confluence of Deep and Rocky Rivers, *Beard 1302* (1956) (NCU); near U.S. 15–501, Rocky River, *Radford 44620* (1963) (NCU). **Durham Co.:** 1.7 mi. N of Weaver, Eno River, *Ahles and Bozeman 57977* (1963) (NCU); N of Bragtown, Eno River, *Radford 7371* (1953) (GA, GH, NCU, NHA, NLU, NCSC (2), US); 5 mi. N of Durham, near Christian's Mill, *Blomquist, s.n.* (1953) (DUKE); Chapel Hill, Ballings Creek, *Coker, s.n.* (1929) (NCU). **Edgecombe Co.:** NE of Rocky Mount, Tar River, *Fox and Whitford 17403* (1948) (GH, NCSC). **Franklin Co.:** 2 mi. E of Bunn, Tar River, *Beal 5685* (1960) (NCSC). **Graham Co.:** 0.7 mi SE of Tapoca, Cheoah River, *Radford 11909* (1956) (NCU). **Granville Co.:** 2 mi. SE of Berea, Tar River, *Radford and Ahles 11540* (1956) (MASS, NCU); 3.7 mi. N of Wilton on Dickerson Rd., Tar River, *Ahles and Radford 11514* (1956) (GA, NY, VDB). **Harnett Co.:** SW of Kipling, Hector Creek, *Beal 4323* (1958) (NCSC). **Haywood Co.:** Big Calocoochee River, *Bold, s.n.* (1939) (NCU); near junction of Pigeon River, Fines Creek, *Ahles and Duke 50409* (1958) (NCU); S of Watertown, Pisgah National Forest, *Thomas 31762* (1972) (NLU, SMU (2), TENN); Rt. 40, Fines Creek, *Boufford and Wood 16469* (1975) (NCU). **Johnston Co.:** E of Clayton, Neuse River, *Whitford, s.n.* (1959) (NCSC). **Lee Co.:** N of Comnock, Deep

River, *Whitford, s.n.* (1958) (NCSC). **Macon Co.:** 3 mi. N of Aquore Dam, Nantahala River, *Beal 7202* (1961) (NCSC); SE of Nantahala, Nantahala River, *Radford 5252* (1950) (NCU); 1 mi. S of Gneiss, below falls, Crow Creek, *Clausen and Kezer 5620* (1941) (NY). **Madison Co.:** 1.3 mi. W of Whiterockon, NC 212, *Ahles and Duke 50671* (1958) (FLAS, NCU); 1.0 mi. S of Hot Springs, Spring Creek, *Radford and Radford 7409* (1953) (NCU). **Mitchell Co.:** NW of Toecane, Master's Mill, *Beal 2159* (1961) (NCSC). **Nash Co.:** 1 mi. N of Strickland Cross Road, Tar River, *Beal 4159* (1958) (NCSC); 3.1 mi. NE of Red Oak, Swift Creek, *Beal 4156* (1958) (NCSC). **Orange Co.:** Rt. 70, Eno River, *Ahles and Haesloop 53240* (1960) (LAF, MAINE, MIN, NCU, TENN, VPI, WVA); Pleasant Green Road, Eno River, *Boufford 15073* (1974) (CM, MO, NHA); Duke Forest, New Hope Creek, *Wilbur 17941* (1974) (DUKE); Carrboro, Morgan's Creek, *Hueske, s.n.* (1947) (NCU). **Person Co.:** fast flowing stream, *Hall 15032* (1940) (NY, SMU). **Polk Co.:** N of junction with Green River, Pulliam Creek, *DuMond 1771* (1973) (NCSC). **Richmond Co.:** Rt. 73, below bridge, *Beal 4250* (1958) (NCSC); Mountain Creek, *Whitford and Schumacker, s.n.* (1958) (NCSC). **Rockingham Co.:** 1 mi. E of old NC 14, *Beal 7090* (1961) (NCSC). **Rutherford Co.:** Chimney Rock, Hickory Nut Creek, unknown collector, s.n. (1958) (NCSC). **Stanly Co.:** NE of Oakboro, Big Bear Creek, *Ahles and Leisner 16276* (1956) (FLAS, NCU). **Swain Co.:** 1 mi. N of Lauada, Alaska Creek, *Beal 7205* (1961) (DUKE, NCSC). **Transylvania Co.:** Lower Bearcamp Creek, *Rogers and Shake 62129B* (1962) (DUKE); Bearwallow Creek, *Pyron and McVaugh 791* (1936) (GA); N of Broad, Davidson River, *Beal 5796* (1960) (NCSC); Toxaway Creek, *Hardin 2039* (1960) (NCSC). **Wake Co.:** near Rolesville, granite outcrops, *Deloach and Dukes 36* (1961) (NCSC); NW of Zebulon, Mitchell's Mill, *Blomquist, Channell and Ebert 16754* (1955) (DUKE); at falls, Neuse River, *Massey and Leonard 3260* (1972) (MO, NCU (2), NHA); NE of Rolesville, Little River, *Radford and King 45057* (1966) (APSU, FLAS (2), GA, GH, LAF, MAINE, MICH, MIN, NCU, NY, OKLA, SMU, TENN, US, VDB, VPI, WIS (2), WVA). **Watauga Co.:** 2 mi. E of Boone, south fork New River, *Beal 5958* (1962) (NCSC); S of Boone, Watauga River, *Whitford and Schumacker, s.n.* (1959) (NCSC); 2.4 mi. SW of Todd, New River, *Ahles and Duke 47719* (1958) (NCU). **Wilkes Co.:** Moravian Falls, Moravian River, *Beal 5966* (1962) (NCSC); 1.5 mi. W of Maple

Springs, *Beal 5962* (1961) (NCSC). **Yancey Co.:** 2 mi. E of Bald Creek, Cane River, *Beal 2139* (1961) (NCSC); 2.3 mi. W of Ramsayton, *Ahles and Duke 50784* (1958) (NCU).

OKLAHOMA. **McCurtain Co.:** 9.0 mi. SE of Bethel, Mountain Fork River, near Ward Creek, *Hellquist 14977* (1981) (NHA); Game Preserve, Mountain Fork River, *Love 212* (1966) (OKLA); 6 mi. S of Smithville, Mountain Fork River, *Correll and Mitchell 34387* (1967) (GH, LAF, MICH, NCU, NY, OKLA, US); S of Battiest, Glover River, *Taylor and Taylor 9732* (1972) (MIN, OKLA, SMU); 31 mi. E of Antlers, Little River, *Waterfall 17217* (1966) (GH, MICH, OKLA (2)).

PENNSYLVANIA. **Allegheny Co.:** Buttermilk Falls, *Britton, s.n.* (1898) (CM). **Bedford Co.:** 1 1/8 mi. S of Hyndman, rocky stream, *Berkheimer 21735A* (1962) (CM, PH); 1 7/8 mi. SE of Fishertown, rocky stream, *Berkheimer 12243* (1951) (CM, PH). **Berks Co.:** 0.25 mi. SW of Gibraltar, Allegheny Creek, *Brumbach 670–33* (1933) (FLAS, GH, PH). **Bucks Co.:** Norrisville, *Burk, s.n.* (1872) (PH); Monroe, Delaware River, *Rutt, s.n.* (1885) (PH); 2 mi. NW of Point Pleasant, Tinicum Creek, *Proctor 2671* (1947) (PH). **Chester Co.:** Brinton's Bridge, Brandywine Creek, *Pennell 5109* (1913) (PH (2)); near Downington, Brandywine Creek, *Burk, s.n.* (unknown date) (PH); 1.75 mi. SW of Slonaker, French Creek, *Wherry, s.n.* (1951) (PH (2)). **Cumberland Co.:** 0.5 mi. SE of Williams Grove, Yellow Britches Creek, *Wahl, Potter and Browning 21566* (1965) (LAF (2), PH); Brandtsville, Yellow Britches Creek, *Philbrick 1166* (1982) (NHA). **Delaware Co.:** Chester Heights, West Branch of Chester Creek, *Pennell and Adams 591* (1926) (GH, MO, PH (2)); near Bridgewater Station, Chester Creek, unknown collector, s.n. (unknown date) (PH). **Fulton Co.:** SW of New Grenada, Sideling Hill Creek, *Wherry, s.n.* (1941) (PH). **Lehigh Co.:** Bethlehem, LeHigh River, *Wolle, s.n.* (1838) (CM). **Mercer Co.:** 1.5 mi. W of Mercer, Shenango River, *Shelar, s.n.* (1898) (PH). **Monroe Co.:** near Stroudsburgh, Buttermilk Falls, *Bicknell, s.n.* (1898) (PH); 1 mi. W of Shawnee on Delaware, stream joining with Marshall's Creek, *Glowenke, s.n.* (1936) (PH); W of Dupue Island, Shawnee on Delaware, Delaware River, *Glowenke 4219* (1940) (PH); Water Gap, Delaware River, *Bicknell, s.n.* (1898) (NY, PH); Slippery rock, Tobykanna Creek, *Greene, s.n.* (1858) (PH); below Marshall's Creek, in stream joining Marshall's Creek, *Glowenke 19* (1936) (NY). **Montour Co.:** 6 mi. SE

of Danville, Roaring Creek, *Adams 5897* (1940) (NCU, PH). **Northampton Co.:** Easton, Delaware River, *Burk, s.n.* (1872) (PH (2)); Martin's Creek, *Williamson, s.n.* (unknown date) (NY); east of island, above Martin's Creek, Delaware River, *Van Pelt, s.n.* (1906) (PH). **Perry Co.:** 1.25 mi. NNW of Newport, Buffalo Creek, *Myrtle and Adams 9676* (1970) (PH); 1.0 mi. WNW of Drumgold, Sherman Creek, *Myrtle and Adams 41–2* (1944) (NCU, PH). **Philadelphia Co.:** Byberry, *Martindale, s.n.* (1865) (PH); Rhawn St. Falls, Pennypack Creek, *Hand, s.n.* (1939) (PH). **Pike Co.:** 1.5 mi. S of Dingman's Ferry, Delaware River, *Wahl, O'Neil and Hazzard 19355* (1959) (NCU); High Falls, Dingman's Creek, *Brown and Saunders, s.n.* (1899) (PH); 0.75 mi. NNW of Parker's Glenn, Delaware River, *Wahl, O'Neil and Hazzard 19319* (1959) (PH); Sawkill Falls, *Nash, s.n.* (1909) (NY); near Bushkill, Winona Falls, *Fassett and Calvert 19488* (1938) (GH, MO, MSU, WIS). **Snyder Co.:** N of Beavertown, Middle Creek, *Hotchkiss 7878* (1963) (US). **Tioga Co.:** 1.0 mi. WNW of Tiadaghton, Pine Creek, *Wahl 15844* (1955) (GH, MAINE, NCU, PH); 1.25 mi. S of Ansonia, Pine Creek, *Wahl 17744* (1956) (LAF, PH). **Union Co.:** 5 mi. W of White Deer, White Deer Creek, *Roberts 3167* (1972) (OS, PH). **Venango Co.:** 2.5 mi. NW of Utica, French Creek, *Wahl 18085* (1956) (PH). **Warren Co.:** Warren, Allegheny Creek, *Witz, s.n.* (1930) (CM). **Wayne Co.:** 0.25 mi. below Hancock Bridge, Buckingham Turnpike, west branch of Delaware River, *Dix 560* (1942) (PH); 2.5 mi. SE of Balls Eddy, west branch Delaware River, *Dix, s.n.* (1946) (PH); 1 mi. NE of Equinunk, Delaware River, *Wahl, O'Neil and Regan 19276* (1959) (PH); 3 mi. NNE of Damascus, Delaware River, *Wahl, O'Neil and Regan 19307* (1959) (PH). **York Co.:** 0.75 mi. SSE of Long Level, Fishing Creek, *Moul 10108* (1949) (CM, PH).

RHODE ISLAND. **Providence Co.:** Georgiaville [Smithfield], Woonasquatucket River, unknown collector, *s.n.* (1894) (NEBC); East Providence, Hunt's Mill, Ten Mile River, *Collins, s.n.* (1893) (F, CONN (3), MO, NHA, PH, US).

SOUTH CAROLINA. **Anderson Co.:** Big Generostee Creek, Weems Creek, *Thomas 501A* (1975) (CLEMS); W of Anderson, Tugaloo River, *Radford 18001* (1956) (NCU). **Lancaster Co.:** ENE of Kershaw, S.C. Rt. 265, Lynches River, *Ahles and Haesloop 31313* (1957) (CM, MICH, OKLA, SMU). **Laurens Co.:** state highway 101, Durbin Creek, *Freeman 56921* (1956) (NCU). **Oconee Co.:** S.C. Rt. 59, Beaverdam

Creek, *Kral, s.n.* (1969) (CLEMS); above Westminster, Brasstown Creek, *Taylor 31* (1978) (CLEMS); 3 mi. from S.C. Rt. 11 and 95, behind Station Falls, *Ferguson 51* (1975) (CLEMS); NNE of confluence of Brasstown and Little Brasstown Creeks, *Boufford, Massey and Katz 16990* (1975) (NCU); 0.8 mi. S of North Carolina state line, Thompson River, *Ware and White 3315* (1970) (VDB). **Richland Co.:** I–126, at Candi Lane, Saluda River, *Crow 3274* (1980) (NHA). **Union Co.:** Rt. 49, Fairforest Creek, *Freeman 56631* (1956) (NCU). **York Co.:** E of Clover, Dan Creek, *Ahles 34652* (1957) (NCU).

TENNESSEE. **Blount Co.:** below Cove Creek, Abrams Creek, *Hubbs 19721* (1937) (MICH); 0.1 mi. below Ellejoy Creek, Little River, *Dennis, Nakosteen, Farmer, Comiskey, McNeilus and Patrick, s.n.* (1979) (TENN); 1.5 mi. N of Rocky Branch, Little River, *Webb, s.n.* (1975) (NCSC, TENN). **Bradley-McMinn Co.:** near Patty Branch, Hiawassee River, *Dennis and Wofford, s.n.* (1978) (TENN, TVA). **Cocke Co.:** Wolf Creek, *Sohmer 32477* (1963) (TENN). **Coffee Co.:** near Tullahoma, Rutledge Falls, *Sharp and Clebrch 4724* (1947) (TENN). **Davidson Co.:** Couchville Pike, Stones River, *Edwards, s.n.* (1954) (VDB). **Greene Co.:** Paint Rock, *Redfield 7669* (1876) (MO). **Grundy Co.:** below Altamount, Falls of Collins River, *Svenson 9398* (1938) (GH, PH, SMU, TENN). **Johnson Co.:** Shady Valley, Beaverdam Creek, *Webb and Webb 47150* (1976) (TENN, VDB). **Knox Co.:** E of Knoxville, French Broad River, *Wofford, Holton and Dennis 79–162* (1979) (TENN). **Lauderdale Co.:** Cypress Creek, *Hall, s.n.* (1964) (TVA, UNA). **Lewis Co.:** 7 mi. SE of Hokenwald, *Webb and Price 3091* (1980) (TENN, TVA). **Lincoln Co.:** 5 mi. S of Mulberry, Elk River, *Webb and Price 3167* (1980) (TENN). **Loudon Co.:** between Tolivar and Davis Islands, Little Tennessee River, *Wofford, Dennis and Bates 78–128* (TENN, VDB). **Maury Co.:** W of confluence with Fountain Creek, Duck River, *Webb and Dennis 1696* (1978) (TENN, TVA, VDB). **Monroe Co.:** 6 mi. up stream of Ballplay Park (Sloan Bridge), Tellico River, *Webb and Price 3537* (1980) (TENN, TVA); 0.5 mi. past Doublecamp Creek, campground, Citico Creek, *Malter, s.n.* (1977) (TENN); Rose Island, Little Tennessee River, *Bates, s.n.* (1976) (TVA). **Morgan Co.:** Montgomery Bridge, Emory River, *Robinson, s.n.* (1935) (TENN); NW of Hatfield Mountain, Obed River, *Patrick and Schmalzer 3125* (1981) (TENN). **Perry Co.:** Slink Shoals Ford, Buffalo River, *Webb 4341* (1981) (TENN).

Polk Co.: below Farmer, Rt. 68, Hiawassee River, *Rogers and Bowers 43923* (1969) (TENN, VDB). **Sevier Co.:** West Fork of Little Pigeon River, *Hubbs 19720* (1937) (MICH); Sevierville, Pigeon River, *Svenson 4007* (1930) (F, PH); W of Gatlinburg, Rt. 73, Little River, *Steyermark 65842* (1948) (F). **Swain Co.:** Greak Smokey Mountains National Park, *Ravensford, Barksdale and Tenneson 3109* (1936) (TENN). **Van Buren Co.:** Rockhouse Falls, Cane Creek, *Norris and Sharp 1022* (1951) (DUKE, FLAS, GA, MO, NCSC, NCU, NY, SMU, TENN, UNA, US, WVA). **Wayne Co.:** 10 mi. N of Waynesboro, Rt. 13, Buffalo River, *Webb and Price 1320* (1978) (TENN).

VERMONT. **Chittenden Co.:** South Burlington, Winooski River, *Cook and Barrington, s.n.* (1977) (VT). **Windham Co.:** Jamaica, West River, *Dobbins, s.n.* (1907) (GH). **Windsor Co.:** Woodstock, *"Winslow", s.n.* 1910 (US).

VIRGINIA. **Bedford Co.:** unknown locality, *Curtis, s.n.* (1872) (F, GH, MASS, MIN, OS, US). **Fairfax Co.:** 2 mi. SW of Garfield, Accotink Creek, *Fosberg 18655* (1942) (NO, PH). **Giles Co.:** Pembroke, at Castle Rock, New River, *Wilson, s.n.* (1972) (VPI); near Berton, New River, *Musselman and Musselman 2885* (1969) (SMU, WIS); 1 mi. S of Eggelston, New River, *Marx 2640* (1974) (NLU). **Loudoun Co.:** N of Neersville, Rt. 340, Potomac River, *Ahles and James 61739* (1965) (NCU). **Montgomery Co.:** below Radford Arsenal, New River, *Whitehurst, s.n.* (1972) (VPI). **Prince William Co.:** below Beverley Mill, Broad River, *Allard 8152* (1940) (GH, VPI). **Stafford Co.:** Rt. 1 near Fredericksburg, Rappahannock River, *Webb and Webb 51843* (1976) (TENN, VDB).

WEST VIRGINIA. **Cabell Co.:** 3 mi. above Salt lick, Guyandott River, *Berkeley 431* (1930) (MO). **Calhoun Co.:** below Annamoriah Ferry, *Bartholomew, s.n.* (1944) (FLAS, LSU, NCU, UNA). **Fayette Co.:** 0.25 mi. above mouth of Dowdy Creek, New River, *Grafton, s.n.* (1976) (MIN); near Wardensville, Cacopon River, *Berkeley 1574* (1930) (MO). **Greenbrier Co.:** Alderson, Greenbrier River, *White 1014* (1976) (WVA). **Hampshire Co.:** New Creek, *Smith, s.n.* (1880) (US). **Kanawha Co.:** Upper Falls, Coal River, *Strausbaugh, s.n.* (1931) (WVA). **Lincoln Co.:** near Miller School, unknown collector, *s.n.* (1829) (WVA (2)). **Pocahontas Co.:** Seebert, Greenbrier River, *White 1045* (1976) (WVA). **Raleigh Co.:** Sandstone Falls, New River Gorge, *Grafton and McGraw, s.n.* (1974) (WVA). **Wirt Co.:** shoals below Twelve Pole Creek Bridge, *Plymale 620* (1938) (GH, WVA); 3

mi. above Creston, at mouth of Two Run, Kanawha River, *Bartholomew W1226* (1942) (WVA (2)). **Wyoming Co.:** below Baileysville, Guyandott River, *Morris 1210* (1900) (F, TENN, US).

DOMINICAN REPUBLIC. **Prov. Santiago:** Distr. San José de las Matas, Rio Magua, *Valeur 130* (1931) (F, MO).

HONDURAS. **Dept. of Comayagua:** vicinity of Siguatepeque, *Standley 56071* (1928) (F, US (2)); Siguatepeque, *Rodriguez 2671* (1945) (F).

TRIFOLIUM STOLONIFERUM, RUNNING BUFFALO CLOVER: DESCRIPTION, DISTRIBUTION, AND CURRENT STATUS

RALPH E. BROOKS

Running buffalo clover, *Trifolium stoloniferum* Muhl. ex A. Eaton (Fabaceae) is one of three species of this temperate genus indigenous to the eastern United States. Since this little known and perhaps extirpated species was described in 1818, its distribution has been variously and often erroneously reported and its taxonomic status questioned. While the species was collected with some regularity during the 1800's from eastern Kansas to West Virginia, *T. stoloniferum* has been collected a mere five times since 1900, most recently in 1940 (Webster County, West Virginia). The current interest in rare and endangered species, coupled with the varied literature accounts, led to the current investigation of the characteristics and current status of *T. stoloniferum*.

METHODS

Despite consulting field botanists in the region where *Trifolium stoloniferum* was known to occur and making field excursions to past collection sites, my efforts to locate extant populations of the plant have proven futile. Thus this investigation is based entirely on herbarium specimens and available literature.

Herbaria at more than 50 institutions, as well as several private collections, were consulted during the course of this study. The herbaria consulted are listed according to the acronyms of Holmgren et al. (1981) (an asterisk (*) indicates no specimens found; a double asterisk (**) indicates no response to the loan request): BGSU*, BH**, BHO*, BUT**, CINC, CLM, CM, DS, F, GH, IA, ILL, IND*, IS, ISC, ISM*, ISU**, JHWU, KANU, KE, KNK*, KSC*, KSP*, KSTC*, KY, LYN*, MCA*, MO, MU, MUR*, MUS*, MWI*, NEB, NDG*, NY, NYS, OC, OKL*, OKLA*, OS, PH, PHIL, PUR, SDSU*, SDU*, SIU*, SMS*, SMU*, SWMT*, TENN*, UARK, UCHT*, UMO, US, VDB*, VIP*, VT, WAB**, WVA, YUO, Baldwin-Wallace College, Berea, Ohio*, and Urbana College, Urbana, Ohio*.

TAXONOMIC HISTORY

Henry Muhlenberg originally named *Trifolium stoloniferum* in 1813, in his *Catalogus Plantarum Americae Septentrionalis*. Muhlenberg's new name was, however, invalid since the name was published without a description (nomen nudum). Three years after Muhlenberg's death Amos Eaton published *Manual of Botany for the Northern and Middle States* (ed. 2) and therein validated Muhlenberg's name by publishing a description of the plant. While Eaton (1818) alluded to a type specimen, it was neither clearly designated nor has original material ever been located. In view of this a neotype was recently selected (Brooks, in press).

DESCRIPTION

The majority of botanists describing *Trifolium stoloniferum* have had few specimens from which to work. Eaton (1818) in preparing the original description and McDermott (1910) in his work with North American *Trifolium* each had but a single specimen from which to write his description. As a result past descriptions are generally brief and less than informative. The description which follows was prepared after examining all the specimens discovered during this investigation:

Trifolium stoloniferum Muhl. ex A. Eaton (Fig. 1)

Perennial (probably short-lived), stoloniferous herbs with short subterranean or superficial branching caudex; sometimes with 1 (2) scapose flowering stems from the base; stolons 0.5–3 (6) dm long, rooting at the nodes, glabrous to rarely sparsely puberulent. Leaves basal or alternate on stolons, trifoliate; leaflets obovate to orbicular or obcordate, (8) 20–30 (40) mm long, nearly as wide, glabrous to rarely sparsely pubescent, apex rounded to usually subtruncate and shallowly or evidently retuse, margins serrulate-denticulate; petioles (1) 3–8 (15) cm long, glabrous or puberulent; stipules usually adnate 1/2 or more of length to petiole, lanceolate to ovate-lanceolate, the free portion narrowed to the apex or somewhat abruptly acuminate or cuspidate, glabrous. Flowering stems scapiform, erect, ebracteate, 1–2 from base or solitary from the axils of the stolons, 6–15 (22) cm tall, usually lightly pubescent near the summit, with 2 leaves near the apex; peduncles 1 (2) from the apex of the stem, 2–6 cm long, glabrous to evidently pubescent; inflorescence subglobose,

Figure 1. *Trifolium stoloniferum*.

(1.5) 2.5 3.5 cm diam, with the central axis (2) 4–8 mm long, 20–60 flowered. Flowers 9–12 mm long, soon reflexed; pedicels 2–10 mm long; calyx-tube campanulate, slightly gibbous at the base, 1.5–2.5 mm long, 5-nerved, glabrous or evidently pubescent, the lobes slightly unequal, subulate, (2.5) 3–4 (4.3) mm long, glabrous to pubescent, rarely ciliate; petals white, possibly tinged with pink or purple; standard obovate to obcordate, (8) 9–10 (12) mm long; wings 6 7 mm long, claws 2–3 mm long, ovary short stipitate, elliptic-oblong, 2.5–3 mm long, apically pubescent; ovules 2; style abruptly recurved at the apex, 2.5–3 mm long. Legume oblong, strongly margined, short stipitate, 3–4 mm long, apically pubescent, 1 (2) seeded; seeds dull yellow brown or darker, subreniform, 1.7 2.0 mm long, smooth. Flowering mid-Apr—Jun; fruiting May—Jul.

The habit of *Trifolium stoloniferum* is remotely similar to *T. reflexum* L. and *T. repens* L., a fact attested to by the numerous past reports based on specimens of one or the other of these two species. Gray (1867) wrote of *T. stoloniferum*, "probably a variety of the last [*T. reflexum*]," and most recently Isley (in press) stated, "...one cannot wonder if it [*T. stoloniferum*] is naught an uncommon genetic form of that species [*T. reflexum*]." While admittedly the sample size of *T. stoloniferum* is rather limited, the characters used to distinguish *T. stoloniferum* from *T. reflexum* and *T. repens*, as outlined in Table 1, appear stable.

DISTRIBUTION

When originally named, *Trifolium stoloniferum* was said to occur in Ohio, Kentucky, and Pennsylvania (Muhlenberg, 1813) and Eaton (1816) added western New York. None of these early records can, however, be validated since Muhlenberg's collections were without data and Eaton apparently included the species on another person's word. Of those four states only Kentucky and Ohio were later found to harbor *T. stoloniferum*. Later collections from more western stations increased the known distribution gradually, and sometimes erroneously, with the widest distribution given by Fernald (1950), "W. Va. to S.D., s to Ky., Mo., and e. Kans."

On the basis of specimen evidence accumulated in the present study the range of *T. stoloniferum* may now be modified to include eight states (Fig. 2): Arkansas, Illinois, Indiana, Kansas, Kentucky,

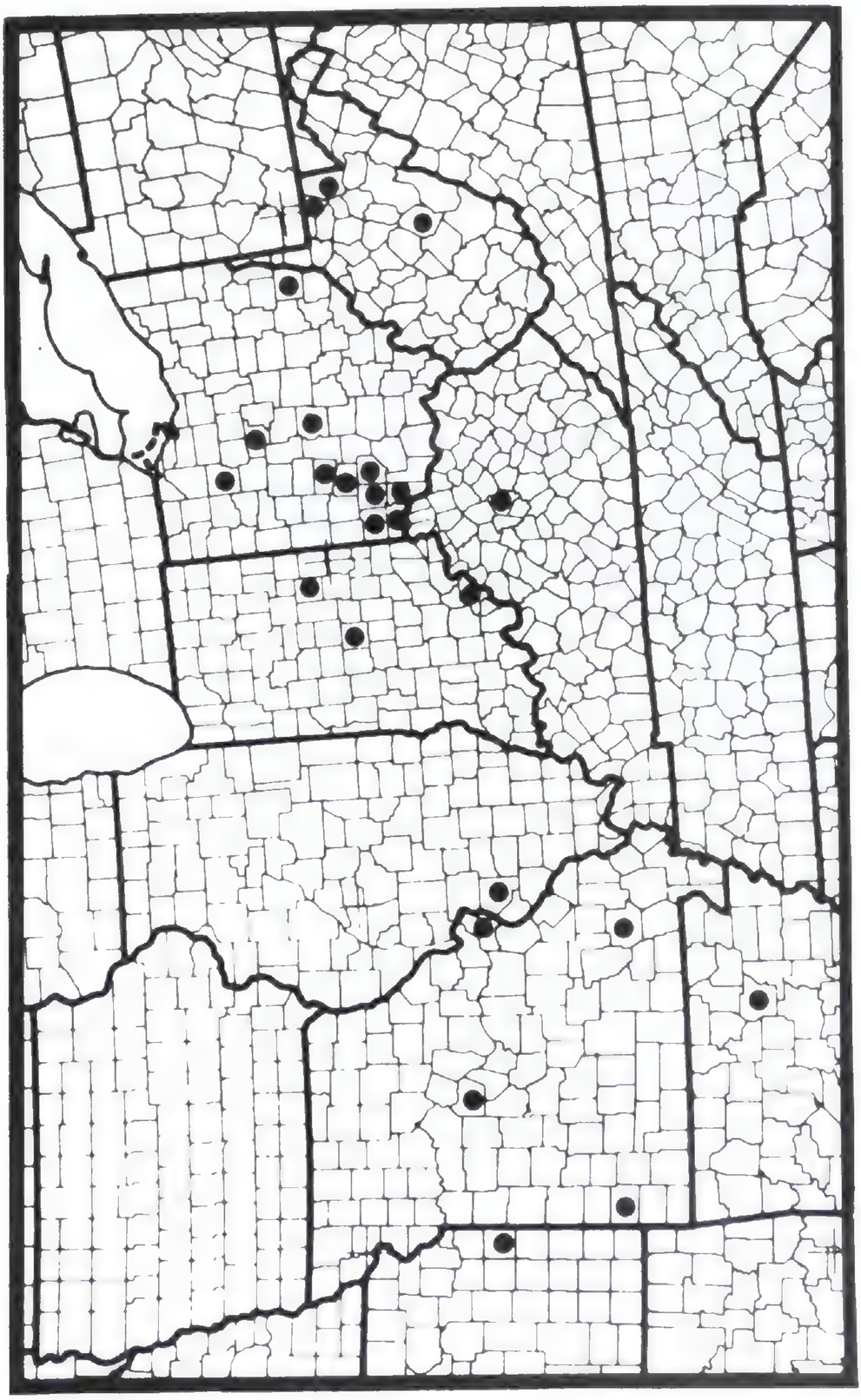

Figure 2. Distribution of *Trifolium stoloniferum*.

Table 1. **Characters distinguishing *Trifolium stoloniferum*, *T. reflexum*, and *T. repens***

Character	*Character States*		
	T. stoloniferum	*T. reflexum*	*T. repens*
1. Habit	stoloniferous	non-stoloniferous	stoloniferous
2. Leaflets	widely obovate to orbicular or obcordate, nearly as wide as long	obovate, oblong, or elliptic, usually much longer than wide	widely obovate to obcordate, nearly as wide as long
3. Flowering Stems	unbranched, scapiform, bearing a pair of leaves in the upper portion and 1 (2) flowering heads from the apex	leafy and frequently branched, 1 to several flowering heads borne from the upper axils	unbranched and naked with a solitary flowering head (a scape)
4. Calyx	calyx-teeth 2–4× as long as the tube	calyx-teeth 2.5–4× as long as the tube	calyx-teeth 1–1.5× as long as the tube
5. Seeds	1.7–2.0 mm long, smooth	1.2–1.5 mm long, obscurely verruculose or with minute irregular ridges	1–1.3 mm long, smooth

Missouri, Ohio, and West Virginia. The earliest dated collection found was made in 1830, near St. Louis, Missiouri, by L. C. Beck. Thereafter, the plant was collected at scattered sites throughout its range, especially in the later 18th century. The two most recent collections were both made in West Virginia, one in 1937, in Preston County and the other in 1940, in Webster County.

Specimen-documented records of *T. stoloniferum* include the following:

ARKANSAS. **Independence Co.:** on railroads, 23 Apr 1896, *H. Eggert s.n.* (MO).

ILLINOIS. **St. Claire Co.:** Cahokia, 1 Jun 1890, *herb. N. M. Glatfelter s.n.* (MO).

INDIANA. **Clark Co.:** Charlestown, May 1880, *herb. A. H. Young s.n.* (PH). **Delaware Co.:** woodlands, May 1882, *W. W. Canby s.n.* (NY). **Marion Co.:** open woods, Jun 1876, *E. F. Shipman s.n.* (F, PH).

KANSAS. **Miami Co.:** 10 Jul 1884, *J. H. Oyster s.n.* (MU); Jul 1885, *J. H. Oyster s.n.* (DS, F, MU, NY).

KENTUCKY. **Fayette Co.:** Lexington, fields, May 1834, *R. Peter s.n.* (NY); 1835, *C. W. Short s.n.* (GH); May (no yr.), *C. W. Short s.n.* (F, KY, NY, PH); 10 May 1882, *W. A. Kellerman s.n.* (KANU, KSC); no date, *C. W. Short s.n.* (CLM, KY, PH).

MISSOURI. **Cooper Co.:** 5 miles above Booneville on the Missouri River, 1883, *Suckley s.n.* (GH, US). **Jasper Co.:** Carterville, common along streams, 21 May 1907, *B. F. Bush 561* (MO). **St. Louis Co.:** near St. Louis, 1830, *L. C. Beck s.n.* (NYS); Allenton, May 1880, *G. W. Letterman s.n.* (GH); big spring near Allenton, 15 May 1880, *J. H. Kellogg s.n.* (NY); Allenton, alt. 500 ft., 10 May, 1882, *G. W. Letterman s.n.* (F, NY NEOTYPE, PH, UMO, US); Allenton, 16 Jul 1885, *J. H. Kellogg s.n.* (MO); May 1887, *G. W. Letterman s.n.* (F); 20 May 1896, *G. W. Letterman s.n.* (NY); Eureka, Clifly Creek, 18 May 1901, *J. H. Kellogg s.n.* (MO, US). **Wayne Co.:** woods north of Williamsville, 16 May 1893, *H. Eggert s.n.* (MO).

OHIO. **Belmont Co.:** Barnesville, 20 May 1906, *E. E. Laughlin s.n.* (OS); edge of Stur's woods, low ground, *E. E. Laughlin 999* (KE); 22 May 1907, *E. E. Laughlin s.n.* (GH). **Butler Co.:** Oxford, 1887, *J. F. James s.n.* (OS). **Clark Co.:** Springfield, 1878, *E. J. Spence s.n.* (OS); Jun 1882, *H. Martin s.n.* (JHWU). **Clermont Co.:** Miamiville, 25 May 1877, *J. F. James s.n.* (OS); no date, *J. F. James s.n.* (US); Batavia Junc., 22 May 1884, *J. F. James s.n.* (CINC). **Clermont-Warren Cos.:** Loveland, Jul 1877, *D. L. James s.n.* (ILL). **Clinton Co.:** Wilmington, 1876, *D. L. James s.n.* (OS). **Franklin Co.:** Columbus, insane asylum grounds, 1890, *A. D. Shelby s.n.* (OS); 8 Jun 1882, *W. S. Devol s.n.* (OS); 27 May 1895, *W. A. Kellerman s.n.* (OS). **Greene Co.:** Yellow Springs, 24 May 1870, *herb. J. Y. & T. L. Bergen s.n.* (G). **Hancock Co.:** Williamstown, 1834, *herb. J. P. Paddock s.n.* (ILL). **Hamilton Co.:** Spring Grove, Cincinnati, 9 May 1878, *J. F. James s.n.* (OS); Mt. Echo, Cincinnati, 1878, no collector (CINC); near Cincinnati, 15 May 1880, *C. G. Lloyd s.n.* (PH, US); 1881, *C. G. Lloyd s.n.* (US); 25 May 1882, *C. G. Lloyd s.n.* (NYS); 3 Jun 1883, *C. G. Lloyd s.n.* (PH); 3 Jun 1884, *C. G. Lloyd s.n.* (CINC); 21 May 1886, *C. G. Lloyd s.n.* (CINC, ILL, OC); 27 May 1888, *C. G. Lloyd s.n.* (MO); Cincinnati, 31 May 1879, *herb. A. P. & L. V. Morgan s.n.* (NY, US); no local, 1 Jun 1882, *T. H. Kearney, Jr. s.n.* (OS); North Bend, fernbank in woods along Ohio River, no date, *C. W. Short s.n.* (MO); Ferris Woods, dry fields, no date, *herb. E. L. Braun s.n.* (US).

WEST VIRGINIA. **Monongalia Co.**: Manilla, 29 Jun 1905, *J. L. Sheldon 1640* (WVA). **Preston Co.**: Cheat River, 6 Jun 1937, *Mr. & Mrs. H. A. Davis 924* (private collection of H. A. Davis, Freeport, FL). **Webster Co.**: Back fork of Elk River in dry open woods, 6 Jun 1940, *Mr. & Mrs. H. A. Davis 3748* (WVA).

Erroneous and Undocumented Records

In evaluating the distribution of *Trifolium stoloniferum* it is felt that discounting erroneous records is of some significance. Therefore the following list of erroneous or undocumented reports is presented with reference to where the report was made and the reason for its dispensation. An asterisk (*) following the state indicates that *T. stoloniferum* is documented from another station in the state.

ILLINOIS*

Isley (in press): Augusta (Mercer Co.), based on *T. reflexum*.

IOWA

Rydberg (1932), Steyermark (1963): no specimen documentation; the sheets found (Iowa City, Jun 1889, *Hitchcock* (F); Iowa, Jul 1865, Mary Treat Coll. (MUS)) were *T. reflexum*.

Fitzpatrick (1899), Pammel (1896): Woodbury County, based on *T. repens*.

KANSAS*

Gates (1940): Linn County, no specimen documentation.

Great Plains Flora Association (1977): Rush and Crawford counties, based on specimens of *T. repens* and *T. hybridum*, respectively.

MICHIGAN

No literature reports were found but several specimens of *T. repens* were erroneously determined.

MISSOURI*

Steyermark (1963): Boone County, based on *T. stoloniferum* from Cooper County; Jackson County, based on a collection from Independence County, Arkansas.

MONTANA

Great Plains Flora Association (1977): Rosebud County, based on *T. repens*. Booth and Wright (1966) do not list the species.

NEBRASKA

Peterson (1912): Cass and Lancaster counties, based on *T. repens*.

Great Plains Flora Association (1977): Cherry and Grant counties, based on *T. hybridum*.

NEW YORK

Eaton (1818), Beck (1833): western New York without specimen documentation.

Gilbert (1884): Deerfield, Oneida County, based on *T. reflexum* according to House (1924).

OKLAHOMA

Stemen and Myers (1937), Steyermark (1963): no specimen documentation. Waterfall (1969) does not list the species.

PENNSYLVANIA

Muhlenberg (1813): Muhlenberg's specimens at PH have no collection data, thus his report cannot be verified.

Other specimens examined from the state were *T. reflexum* or *T. repens*.

SOUTH DAKOTA

Rydberg (1932): at MO are two sheets, the first "Sow Prairies, Brookings, 10 Jun 1892, *Thornber*," a fragment of *T. beckwithii* Brewer ex S. Wats. The second is labeled "Flora Nebraskana, Bad Lands, Jul 1844, *F. V. Hayden*," but was most likely collected in the present day Bad Lands of South Dakota. The specimen is *T. stoloniferum* but since habitat such as necessary to support the species does not exist in that area it would appear the specimen was erroneously labeled and should be ignored. Van Bruggen (1976) does not list the species.

TENNESSEE

Chapman (1897), Gleason and Cronquist (1963), Small (1933): no specimen documentation.

TEXAS

While literature reports were not found, several sheets of *T. repens* from the Houston and Dallas vicinities were erroneously labeled *T. stoloniferum*. Correll and Johnston (1970) do not list the species.

VERMONT

Perkins (1888): no specimen documentation.

WISCONSIN

No literature reports were found but several specimens of *T. repens* were erroneously determined.

WYOMING

Great Plains Flora Association (1977): Weston County, based on *T. hybridum*.

CANADA

No literature reports found but specimens of *T. hybridum* were found to be erroneously determined.

HABITAT

Specimen data and literature accounts suggest that *Trifolium stoloniferum* most frequently grew in woodlands associated with water courses. Nearly all the specimens provided with adequate locality data came from stations within the drainage basins of the lower Missouri River and Ohio River. Open habitats, e.g. fields, were only referred to a few times and only in one case is a site thought to represent an accidental introduction (Independence County, Arkansas).

The preference of *Trifolium stoloniferum* for woodlands is further corroborated by Mr. H. A. Davis, Freeport, FL, (pers. comm., 1982), the person last known to collect the plant, who described the Preston and Webster county sites as well drained sites in woodlands.

ABUNDANCE

Trifolium stoloniferum was apparently exceedingly local in its occurrence, being known from fewer than 30 sites scattered in 8 states. The possible exception may have been west-central and southwest Ohio where at least nine stations are known to have existed.

It seems obvious that in the latter 18th century while populations of the clover were limited and widely scattered, a good majority must have been quite vigorous. Repeated collections from the same localities over a series of years substantiate this statement. Shortly thereafter, however, the number of collections dwindled rapidly with a mere five sites documented after 1900, three before 1910 and one each in 1937 and 1940. It might be hypothesized that the habitat destruction resulting from the industrial revolution and the inability of *Trifolium stoloniferum* to adapt to changing environmental stresses led to the demise of the species.

CURRENT STATUS

Over 40 years have now elapsed since *Trifolium stoloniferum* was last collected in Webster County, West Virginia, and more recent sightings of the species are unknown to me. Field trips have been made to several sites in Missouri and east-central Kansas without successfully locating extant populations of the plant.

On this basis one can only presume that *Trifolium stoloniferum* is at the very least an endangered species existing in a few as yet undiscovered sites or the species may in fact be extirpated from its range.

Currently *Trifolium stoloniferum* is not listed as an endangered or threatened species by the U. S. Department of the Interior, Fish and Wildlife Service (Fed. Reg. 82495; 50 CRF 17.11 and 17.12). The species was apparently overlooked in previous listing but has now been nominated for review and, presumably, inclusion in future listings.

ACKNOWLEDGMENTS

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LITERATURE CITED

BARKLEY, T. M. 1968. Manual of the Flowering Plants of Kansas. Kansas St. Univ. Endowment Assoc., Manhattan.

BECK, L. C. 1833. Botany of the Northern and Middle States. Webster & Skinners, Albany, New York.

BOOTH, W. E., & J. C. WRIGHT. 1966. Flora of Montana (ed. 3). Dept. Bot. & Microbiol., Montana St. Univ., Bozeman.

BROOKS, R. E. Neotypification of *Trifolium stoloniferum* Muhl. ex. A. Eat. (Fabaceae). Taxon (in press).

CHAPMAN, A. W. 1897. Flora of the Southern United States (ed. 3). American Book Co., New York.

CORRELL, D. S., & M. C. JOHNSTON. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.

EATON, A. 1818. Manual of Botany for the Northern and Middle States (ed. 2). Webster & Skinners, Albany, New York.

FERNALD, M. L. 1950. Gray's Manual of Botany, Fifth Edition. American Book Co., New York.

FITZPATRICK, T. J. 1899. Manual of the Flowering Plants of Iowa. Part 1. Polypetalae. Privately published by the author.

GILBERT, B. D. 1884. Notes on botrychia. Bull. Torrey Bot. Club **11**: 75–76.

GLEASON, H. A., & A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand Co., Inc., Princeton, New Jersey.

GRAY, A. 1867. Manual of Botany of the Northern United States, Fifth Edition. Ivison, Blakeman & Co., New York.

GREAT PLAINS FLORA ASSOCIATION. 1977. Atlas of the Flora of the Great Plains. Iowa St. Univ. Press, Ames.

HOLMGREN, P. K., ET AL. 1981. Index Herbariorum. Part I, The Herbaria of the World (ed. 7). Dr. W. Junk B. V., Publishers, The Hague.

HOUSE, H. D. 1924. Annotated list of the Ferns and Flowering Plants of New York State. N. Y. St. Mus. Bull. No. **254**.

ISLEY, D. The Leguminosae of the United States. Subfamily Papilionoideae: Tribe Trifolieae. Mem. New York Bot. Gard. (in press).

MCDERMOTT, L. F. 1910. An Illustrated Key to the North American Species of *Trifolium*. San Francisco.

MUHLENBERG, G. H. E. 1813. Catalogus Plantarum Americae Septentrionalis Hucusque Cognitarium Indigenarum et Circurum. W. Hamilton, Lancaster, Pennsylvania.

PAMMEL, L. H. 1896. Notes on the flora of western Iowa. Contrib. Bot. Dept. Iowa Coll. Agric. & Mech. **1**: 107–135.

PERKINS, G. H. 1888. Catalogue of the Flora of Vermont. Privately published by the author.
PETERSON, N. F. 1912. Flora of Nebraska. Privately published by the author.
RYDBERG, P. A. 1932. Flora of the Prairies and Plains of Central North America. The New York Botanical Garden, New York.
SMALL, J. K. 1933. Manual of the Southeastern Flora. Science Press Printing Corp., Lancaster, Pennsylvania.
STEMEN, T. R., & W. S. MYERS. 1937. Oklahoma Flora. Harlow Publ. Corp., Oklahoma City.
STEYERMARK, J. A. 1963. Flora of Missouri. Iowa St. Univ. Press, Ames.
VAN BRUGGEN, T. 1976. The Vascular Plants of South Dakota. Iowa St. Univ. Press, Ames.
WATERFALL, U. T. 1969. Keys to the Flora of Oklahoma (ed. 4). Private published by the author.

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CYTOLOGICAL AND MORPHOLOGICAL OBSERVATIONS IN *GALINSOGA* AND RELATED GENERA (ASTERACEAE)

JUDITH M. CANNE

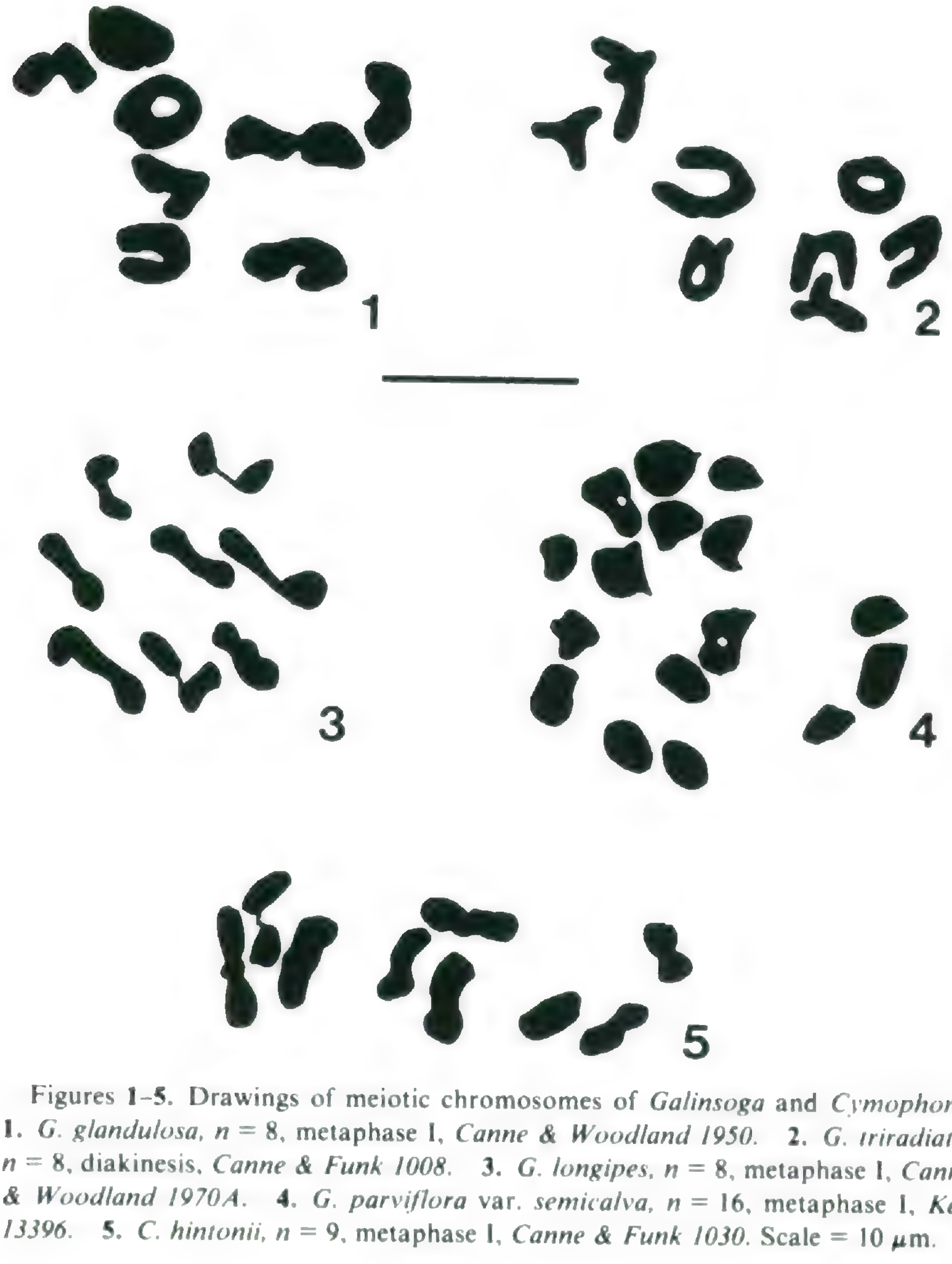
ABSTRACT

Chromosome counts are provided for numerous populations representing nine taxa of *Galinsoga*, one species of *Cymophora*, two species of *Sabazia* and one of *Tridax*. Four of the counts for *Galinsoga* and one for *Cymophora* are newly reported. Morphological observations are offered for several of the species known previously only from type specimens or from few collections. Taxonomic ramifications of the cytological and morphological data are discussed.

Since the appearance of recent taxonomic works concerning *Galinsoga* Ruiz and Pavon (Canne, 1977a) and *Cymorphora* B. L. Robins. (Turner & Powell, 1977) field work in Mexico has yielded collections of poorly known members of these genera in addition to species of the closely related *Sabazia* Cass. and *Tridax* L. Chromosome counts for these Mexican collections are indicated in Table 1 along with a few counts from other regions. Discussion of the taxonomic significance of the cytological observations are included below where pertinent. Morphological observations are added for certain members of the genera that have been known only from type collections or from a small number of collections.

MATERIALS AND METHODS

Buds were fixed in the field in modified Carnoy's fluid (chloroform:absolute ethanol:acetic acid, 4:3:1) and later transferred to 70% ethanol for laboratory storage. Whole buds of capitula were stained for at least 24 hours in Snow's stain before disc florets were squashed in Hoyer's solution for observation of meiotic stages. Root tips for mitotic observations were obtained by germination of achenes on moist filter paper in petri plates. Harvested root tips were treated in a cold, saturated, aqueous solution of paradichlorobenzene for 3–4 hours, fixed for at least 1 hour in a solution of ethanol:chloroform:acetic acid (3:1:1) and then treated as described above for buds. Drawings of all counts were made at a magnification of 2500× with a Zeiss drawing device. Voucher specimens are on deposit at OAC. Scanning electron micrographs of achenes were made at 25Kv on a Jeol JSM–35C scanning electron microscope.



Figures 1–5. Drawings of meiotic chromosomes of *Galinsoga* and *Cymophora*. **1.** *G. glandulosa*, $n = 8$, metaphase I, *Canne & Woodland 1950*. **2.** *G. triradiata*, $n = 8$, diakinesis, *Canne & Funk 1008*. **3.** *G. longipes*, $n = 8$, metaphase I, *Canne & Woodland 1970A*. **4.** *G. parviflora* var. *semicalva*, $n = 16$, metaphase I, *Keil 13396*. **5.** *C. hintonii*, $n = 9$, metaphase I, *Canne & Funk 1030*. Scale = 10 μm.

RESULTS AND DISCUSSION

Galinsoga section **Elata**

Of the four species in sect. *Elata* only *Galinsoga durangensis* (Longpre) Canne has been known from collections other than those from the type locality. The $n = 8$ count reported here for *G. durangensis* confirms previous reports, and was made from a collection at the type location. A recent search for populations of *G. formosa*

Canne proved unsuccessful, and *G. formosa* and *G. mollis* McVaugh remain unknown cytologically.

When first described, *Galinsoga elata* Canne was known only from a single collection locality in Queretaro. Four additional collections were made recently from near this area. Counts from three of these populations confirm the single previous count and establish the base chromosome number as $x = 8$. In the field, plants of *G. elata* are usually less than 0.5 m tall and are often less than 0.1 m tall. Under greenhouse conditions, however, plants assume heights of over 2 m. Field plants of the related *G. mollis* and *G. formosa* are known to reach 1.5 m and 1.0 m respectively.

Galinsoga section **Stenocarpha**

The chromosome number of *Galinsoga filiformis* (S. F. Blake) Canne was reported first as $n = 8$ (Turner 1965, as *Stenocarpha*) then later as $n = 9$ (Solbrig et al., 1972, as *Stenocarpha*). Additional counts reported here from collection *1038* by *Canne and Funk* were $n = 8$ pairs and $n = 8$ pairs plus one supernumerary pair. The small supernumerary pair appears to proceed normally through meiosis and probably accounts for the $n = 9$ count reported by Solbrig, et al. (1972). Mitotic preparations from root tips of germinated achenes from a second population *(Canne & Funk 1044)* yielded counts of $2n = 16$ and an occasional $2n = 16 + 2$ small supernumeraries (Table 1).

Galinsoga section **Galinsoga**

In a recent revision of *Galinsoga* (Canne, 1977a) three new species, *G. glandulosa, G. triradiata* and *G. longipes,* were described from south central Mexico. As noted in the revision, *G. glandulosa* is somewhat anomolous in the genus with its triangular dentate leaves, glandular anther appendages, and weakly cuspidate, ciliate paleae. Known previously only from the type specimen, this species is reported here to have a haploid number of $n = 8$, (Fig. 1, Table 1).

The relatively poorly known, but morphologically distinctive, *Galinsoga triradiata* was counted from two populations as $n = 8$ and $2n = 16$ (Fig. 2, Table 1). At the time of its original publication *G. triradiata* was known only from specimens having epappose achenes. Although these epappose achenes may be glabrous, they

Table 1. **Chromosome numbers of *Galinsoga, Cymophora, Sabazia* & *Tridax*.**

Taxon[1]	Count	Voucher (OAC)[2]	Locality[3]
Galinsoga Ruiz & Pavon			
G. durangensis (Longpre) Canne	$n = 8$	*C & F 1051*	Durango:7.5 mi. NE of Revolcalderos.
G. elata Canne	$2n = 16$	*C & W 1940*	Queretaro:4.4 km. SW of Pinal de Amoles.
	$2n = 16$	*C & W 1942*	Queretaro:1.3 km. NE of Pinal de Amoles.
	$2n = 16$	*C & W 1944*	Queretaro:1.5 km. NE of Pinal de Amoles.
G. filiformis (S.F. Blake) Canne	$n = 8$, $n = 8 + 1$ supernumerary pair	*C & F 1038*	Sinaloa:Mex. 40, 1.7 mi. SW rd. to Santa Lucia.
	$2n = 16$, $2n = 16 + 2$ supernumeraries	*C & F 1044*	Sinaloa:Mex. 40 at jct. rd. to Santa Lucia.
G. glandulosa Canne*	$n = 8$, $2n = 16$	*C & W 1950*	Queretaro:15.6 km. SW of El Madroño.
G. longipes Canne*	$n = 8$	*C & W 1970A*	Mexico:0.7 km. S of Temascaltepec.
	$2n = 16$	*C & W 1971*	Mexico:5.4 km. SW of Temascaltepec.
G. parviflora Cav. var. *parviflora*	$2n = 16$	*C & W 1931*	Morelos:3.1 km. E of Yautepec.

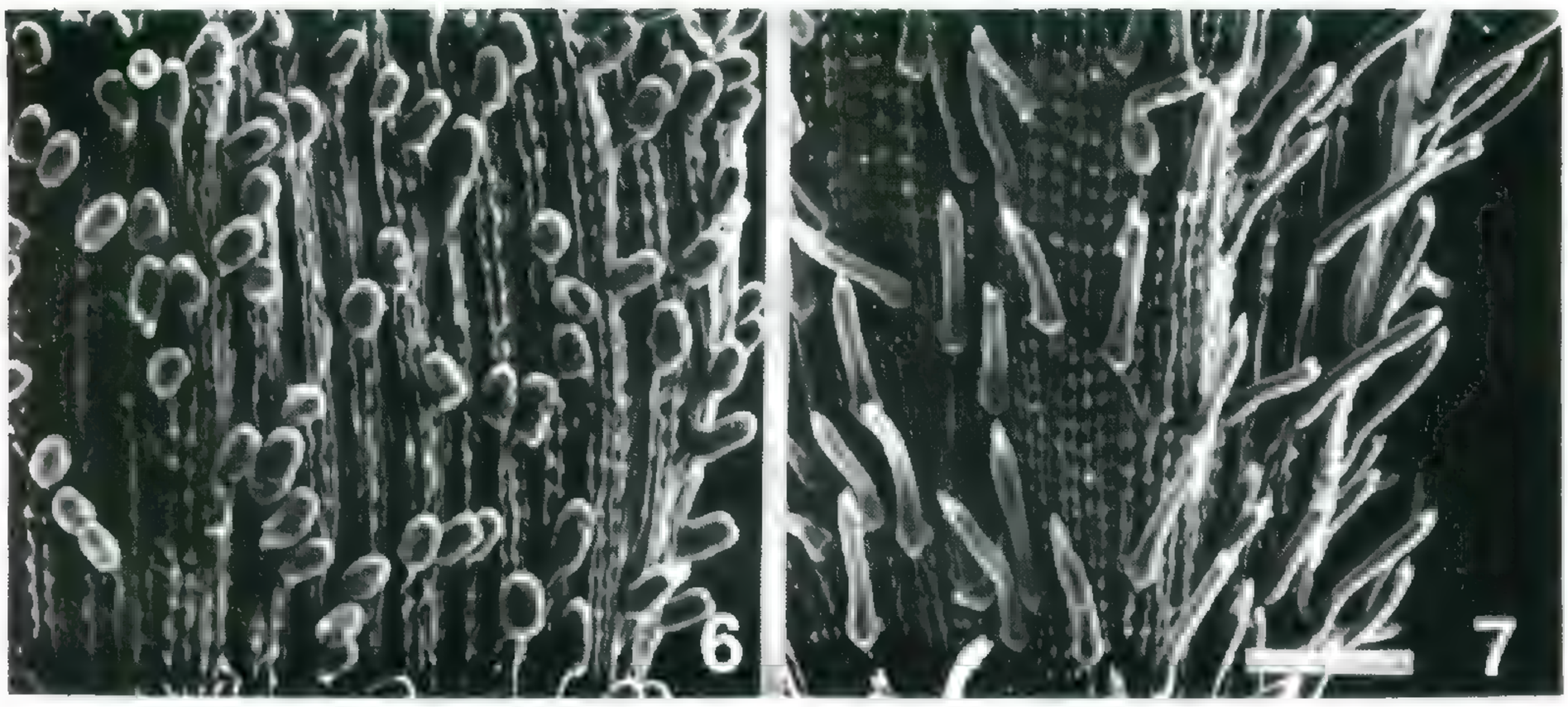
	$2n = 16$	*C & W 1991*	Distrito Federal:1.7 km. NW of Santa Ana Tlacotengo.
	$2n = 16$	*C & W 1992*	Distrito Federal: Xochimilco.
	$n = 8$	*H & F 4270*	Michoacan:10 mi. W of Zamora.
	$n = 8$	*H & F 4228*	Mexico:5 mi. SW of Toluca.
	$2n = 16$	*C 2172*	Australia: New South Wales, Sydney.
	$2n = 16$	*C 2174*	Papua New Guinea:Western Highlands, Mt. Hagen.
	$2n = 16$	*C 2175*	Papua New Guinea:Eastern Highlands, Goroka.
	$2n = 16$	*C 2177*	Papua New Guinea: Morobe, Mt. Kaindi.
G. parviflora Cav. var. *semicalva* A. Gray*	$n = 16$	*D. Keil 13396*	Chihuahua:N side Colonia Garcia.
G. quadriradiata Ruiz & Pavon (representative counts)	$n = 16$, $n = 6_{II} + 20_{I}$ to $10_{II} + 12_{I}$	*C & F 1024*	Michoacan:rd. to Dos Aqua, 9.5 mi S jct. rd. to Coalcomán.
	$2n = 32$	*C & W 1927*	Oaxaca:13.8 km. N of San Jose Pacifica.
	$2n = 32$	*C & W 1945*	Queretaro:1.5 km. NE of Pinal de Amoles.

Table 1. continued

Taxon[1]	Count	Voucher (OAC)[2]	Locality[3]
G. quadriradiata Ruiz & Pavon (representative counts) (continued)	$n = 16$	*C & W 1954*	San Luis Potosi:Mex. 85, 1.2 km. N of Hidalgo border.
	$n = 16, 2n = 32$	*C & W 1970B*	Mexico:0.7 km. S of Temascaltepec.
	$n = 16$	*H & F 4216*	Guerrero:5 mi. E of Taxco.
	$n = 16$	*H 3900*	Panama:Chiriqui:between Horqueta and Cerro Horqueta.
G. triradiata Canne*	$n = 8, 2n = 16$	*C & F 1008*	Michoacan:8.8 mi. E of Uruapan.
	$2n = 16$	*C & F 1011*	Michoacan:7.7 mi. N of Barranca Honda, S of Uruapan.
Cymophora B. L. Robins.			
C. hintonii Turner & Powell*	$n = 9, 2n = 18$	*C & F 1030*	Michoacan:17 mi. W of Villa Victoria.
Sabazia Cass.			
S. humilis (H.B.K.) Cass.	$n = 4$	*C & W 1883*	Mixico:SE of Amecameca.
	$2n = 8$	*C & W 1961*	Mexico:Mex. 15, 4.1 km. E jct. rd. to Ocoyoacac.

	$2n = 8$	*C & W 1962*	Mexico:6.6 km. SW of jct. Mex. 134 & Mex. 130.
	$2n = 8$	*C & W 1964*	Mexico:3.2 km. NE of San Francisco Oxtotilpan.
	$2n = 8$	*C & W 1976*	Mexico:Palo Mancornado.
	$2n = 8$	*C & W 1989*	Morelos:Mex. 95, 9.8 km. S of Distrito Federal border.
S. liebmannii Klatt	$2n = 48$	*C & W 1922*	Oaxaca:6.4 km. N of San Jose Pacifica.
	$2n = 48$	*C & W 1929*	Oaxaca:15.1 km. N of San Jose Pacifica.
Tridax L.			
T. mexicana A. M. Powell	$n = 9$	*C & F 1016*	Michoacan:5.1 mi. N of Barranca Honda, S of Uruapan.
	$2n = 18$	*C & W 1895*	Puebla:9.7 km. N of Jualillos.
	$2n = 18$	*C & W 1897*	Puebla:3 km. S of Salitrillo.

[1]Asterisk indicates new count.
[2]C = J.M. Canne, F = V. Funk, H = R. Hartman, W = D. W. Woodland.
[3]Localities are from Mexico unless indicated otherwise.



Figures 6 & 7. Scanning electron micrographs of achenes of *Galinsoga triradiata*. Fig. 6. Short, blunt trichomes on epappose achene *(Canne & Funk 1008)*. Fig. 7. Elongate, bifid trichomes on pappose achene *(Canne & Funk 1011)*. Scale = 100 μm for both figures.

usually bear a slight to dense pubescence of reddish colored, short, blunt trichomes that are characteristic of the species (Fig. 6).

One of the recent collections *(Canne and Funk 1011)* contains individuals with epappose achenes and individuals with pappose achenes. All achenes on nineteen plants of a second collection *(Canne and Funk 1008)* are entirely epappose. The curiosity here is not that pappose achenes exist, but that the peculiar trichomes typical of *Galinsoga triradiata* are not present on pappose achenes. These achenes, like those in other species of the genus, have trichomes composed of two unequal, elongate cells (Fig. 7). The pappus of disc achenes consists of 15 to 20 obtuse to acuminate, obovate, fimbriate, white scales. The pappus is either lacking on ray achenes or is composed of a few reduced scales, a situation characteristic of several other species of *Galinsoga* as well.

Galinsoga longipes, a species similar in many regards to *G. triradiata* (Canne, 1977a), also has $n = 8$ and $2n = 16$ (Fig. 3, Table 1). This taxon is the diploid most similar morphologically to the tetraploid weedy *G. quadriradiata* Ruiz and Pavon. Collections *1970 A* and *B* by *Canne and Woodland* from a single mixed population consist of *G. longipes* and the morphological variant of *G. quadriradiata* characterized by white rays, tall narrowly conic receptacle, shallowly trifid paleae, eglandular trichomes, and peduncles averaging longer than 2 cm. This is the variant of *G. quadriradiata* morphologically most similar to the diploid *G. longipes*. All counted

specimens of *G. quadriradiata* and *G. longipes* from this mixed population were $n = 16$ (or $2n = 32$) and $n = 8$ respectively. There is no cytological or morphological evidence to indicate hybridization and the formation of triploids or higher order polyploids between these two apparently closely related taxa.

The representative counts reported here at $n = 16$ and $2n = 32$ for *Galinsoga quadriradiata* are consistent with previous records for plants from Mexico and Central America (Table 1). In addition, eight populations from Michoacan, three from Mexico, two each from Hidalgo and Oaxaca, and one each from Guerrero, Puebla, Queretaro, and Sinaloa were counted at $n = 16$ or $2n = 32$. Voucher data are available from the author. Canne (1977a) noted earlier that there are at least three internally variable morphotypes of *G. quadriradiata* and that hybrids among them abound. The reduced male fertility and meiotic irregularities in the hybrids, however, indicate that these morphological variants are not fully compatible sexually (Canne 1977a).

Collection *1024* by *Canne and Funk* from western Michoacan offers an illustration of the interbreeding of two of these morphotypes of *G. quadriradiata*. Among the 19 plants collected from this population were 7 specimens of a variant typified by ray corollas that turn pink when dried and are deeply trilobed; ray achenes 1.4–1.9 mm long; paleae essentially entire and 0.5 mm or less in width; achenes epappose; peduncles with abundant glandular-tipped trichomes; disc florets 20 or fewer per head. Nine specimens of the second variant are characterized by ray corollas that remain white when dried and are shallowly trilobed; ray achenes 1.2–1.5 mm long; paleae irregularly trifid and 0.5 to 1.1 mm in width; achenes pappose; peduncles with eglandular trichomes; disc florets usually 25 to 35 per head. Pollen stainability in lactophenol cotton blue ranged from 67% to 94% for the pink rayed variant and from 69% to 97% for the white rayed variant.

Among the 19 plants three appear to be f_1 hybrids having an intermediate morphology characterized by ray corollas tinged with pink; paleae within a head entire to irregularly trifid; achenes epappose or with a short pappus; and sparse to dense peduncular pubescence of glandular trichomes. Pollen stainability ranges from 12% to 27% for these plants. The majority of pollen grains are empty, very small or malformed. Few mature, black achenes were produced,

generally only 1 to 3 per head. Meiosis in the presumed hybrids was irregular with the formation at metaphase I of 6 bivalents and 20 univalents to 10 bivalents and 12 univalents. Lagging chromosomes, anaphase bridges, and the production of micronuclei were common.

All parental types and hybrids of the variants of tetraploid *Galinsoga quadriradiata*, including those from collection *1024*, grown under greenhouse conditions were self compatible. Bagged heads set full complements of fruit in parental types but produce reduced set in hybrid plants. The self and cross-compatibility of the variants of *G. quadriradiata* and the viability of hybrid achenes have in part lead to the mosaic of morphological variation seen in this species in Mexico (Canne, 1977a). The mode of origin of the Mexican tetraploid morphotypes is not known. The presence of at least three morphological variants that are only partially sexually compatible could have resulted from alloploid origins with the sharing of at least one parent among the variants.

All specimens of typical *G. parviflora* Cav. that have been counted to date are diploids at $n = 8$ (Canne, 1977a, and Table 1). I have accepted as synonomous with *G. parviflora* a morphological variant that has paleae more shallowly trifid, smaller leaves and a stricter growth habit than are usual for typical *G. parviflora*. This variant, *G. parviflora* Cav. var. *semicalva* A. Gray, occurs primarily in Arizona, New Mexico, and neighboring regions of Chihuahua. The overlap in distribution and morphological intergradation with typical *G. parviflora* prompted me to treat these plants informally as variants until more was known of them (Canne 1977a). A count reported here for this variant as $n = 16$ lends credence to the opinions of Gray (1853) and St. John and White (1920) that formal recognition is appropriate. Accordingly, the tetraploid is listed in Table 1 as *G. parviflora* Cav. var. *semicalva* A. Gray.

Cymophora

This small genus has met with considerable attention of late because of its purported taxonomic position between *Tridax* and *Galinsoga* (Turner, et al., 1973; Turner & Powell, 1977; Canne, 1977b). The chromosome number of *Cymophora hintonii* Turner and Powell is reported for the first time here as $n = 9$ from a single collection in Michoacan near the Colima border (Fig. 5, Table 1). Root tips from germinated achenes repeatedly yielded counts of $2n = 18$. Of the four species of *Cymophora* the only other taxon for

which a chromosome number is known is *C. pringlei* B. L. Robins with $2n = 16$ (Turner et al., 1973). Thus, if *C. hintonii* is uniformly $n = 9$, the genus is dibasic at $x = 8$ and 9.

Interestingly, there are now counts for one species from each of the species pairs in the genus. *Cymophora accedens* (S. F. Blake) Turner & Powell and *C. pringlei* ($n = 8$) have ovate to ovate-lanceolate leaf blades on short petioles, phyllaries and paleae with a few pronounced veins, and moderately to densely pubescent disc achenes. In contrast, *C. hintonii* ($n = 9$) and *C. venezuelensis* (Arist. & Cuatr.) Canne have long petiolate, ovate to trullate blades of a thinner texture with coarsely, irregularly serrate to shallowly lobed margins. The phyllaries and paleae are striated and have numerous, inconspicuous veins. The achenes are glabrous to only slightly pubescent. Whether the congruence of the two morphologies with the two chromosome numbers is a reflection of two phyletic units among the four species as suggested by Robinson, et al. (1981) will be more easily evaluated when the chromosome numbers become known for *C. accedens* and *C. venezuelensis*. The quandry over whether this small genus is more closely allied to *Tridax* ($x = 9, 10$), where two species were formerly placed, or to *Galinsoga* ($x = 8$) or *Sabazia* ($x = 8$) is not resolved by the $n = 9$ count for *C. hintonii*.

Sabazia and **Tridax**

Counts listed in Table 1 for *Sabazia* and *Tridax* are consistent with previously published reports (Longpre, 1970; Powell, 1965).

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LITERATURE CITED

Canne, J. M. 1977a. A revision of the genus *Galinsoga* (Compositae:Heliantheae). Rhodora **79:** 319–389.

_____. 1977b. A new combination in *Cymophora* (Compositae:Heliantheae: Galinsoginae). Madroño **24:** 190–191.

Gray, A. 1853. Plantae Wrightianae. Texano-Neo-Mexicanae, Part II. Smith-

sonian Contr. Knowl. **5:** 98.

LONGPRE, K. 1970. The Systematics of the genera *Sabazia, Selloa* and *Tricarpha* (Compositae). Publ. Mus. Michigan State Univ., Biol. Ser. **8** (4): 283–384.

POWELL, A. M. 1965. Taxonomy of *Tridax* (Compositae). Brittonia **17:** 47–96.

ROBINSON, H., A. M. POWELL, R. M. KING, & J. F. WEEDIN. 1981. Chromosome numbers in Compositae, XII: Heliantheae. Smithsonian Contr. Botany **52:** 1–28.

SOLBRIG, O., D. W. KYHOS, A. M. POWELL, & P. RAVEN. 1972. Chromosome numbers in Compositae VIII:Heliantheae. Am. Jour. Bot. **59:** 869–878.

ST. JOHN, H., & D. WHITE. 1920. The genus *Galinsoga* in North America. Rhodora **22:** 97–101.

TURNER, B. L. 1965. Taxonomy of *Stenocarpha* (Compositae-Heliantheae-Galinsoginae). Southw. Naturalist **10:** 238–240.

———., & A. M. POWELL. 1977. Taxonomy of the genus *Cymophora* (Asteraceae: Heliantheae). Madroño **24:** 1–6.

———., A. M. POWELL & T. J. WATSON, JR. 1973. Chromosome numbers in Mexican Asteraceae. Amer. J. Bot. **60:** 592–596.

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THE TYPE LOCALITY OF *SENECIO GRACILIS* PURSH

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The type locality of *Senecio gracilis* Pursh is stated by Cronquist (in Barkley, 1978) as: "On the rocky banks of rivers, Pennsylvania.", holotype in BM. Ewan (1979) suggests the typification of *S. gracilis* may require different establishment as the locality stated by Cronquist (in Barkley, 1978) is actually Pursh's field station (Pursh, 1814). The holotype, indicated by Ewan in 1954, and the same specimen seen by Cronquist (pers. comm., 1981), is a specimen in the Banks Herbarium at BM, catalogued by D. Solander, Banks' librarian, under number 28 on page 715 of Solander's manuscript catalog, as *"Senecio strictus"*. Solander states in his catalog that it was received from J. Bartram. Solander cites the range of "Senecio strictus", quoting from Bartram, as "habitat in montosis America septentrionalis". Although this specimen probably originated in Pennsylvania (Bartram furnished Banks a number of Pennsylvania herbarium specimens), Bartram's locality citation stands as the type locality of *S. gracilis*. The type locality of *S. gracilis* can not be limited to Pennsylvania.

The situation is complicated by the fact that the type specimen of *Senecio gracilis* is labeled on the back "Hudson's Bay: Albany Fort, 1781", collector unknown. Labeling on the back of herbarium sheets was a frequent custom of the 18th century. The type specimen of *S. gracilis* is of a morphology unknown from Hudson Bay but frequent in Pennsylvania. It is reported by Bartram in Solander's catalog as flowering in May, much too early for a Hudson Bay *Senecio* but timely for a Pennsylvania specimen. The possibility of confused labeling of the Pursh type specimen must be considered.

There are two other specimens in the Solander catalog of the Banks Herbarium, both under number 27 on page 715, which are labeled on the back "Hudson's Bay, 1773", collector unknown, and which appear to be duplicates. Both are annotated *Senecio pauperculus* Michx by Ewan, and I concur. Both specimens are entered by Solander in his catalog as received from Bartram, who assigned them the same locality as that for the type specimen of *S. gracilis*. Both specimens are probably from Pennsylvania, with the Hudson

Bay label probably affixed in error. Solander included both specimens in his "*Senecio strictus*", though these and the type specimen of *S. gracilis* are obviously different taxa.

A fourth specimen catalogued by Solander as "*Senecio strictus*" was collected by J. Banks in Newfoundland in 1766. Someone wrote the name *S. gracilis* on the sheet but it was later annotated as *S. pauperculus* by J. Greenman. Lysaght (1971) dismissed this specimen from consideration as the type *S. gracilis* since it did not originate with J. Bartram as cited in Solander's protolog of "*Senecio strictus*".

The reason I have delineated the type locality of *Senecio gracilis* is that I believe its modern equivalent, *S. aureus* var. *gracilis* (Pursh) Hook., should be recognized despite its submergence by Barkley (1962, 1978). Barkley (1962) first proposed this submergence with reservation, recommending the variety be restudied.

What I have seen of this variety in the field (Virginia) reveals a distinct biotype, characterized by reduced elongate, ovate, cuneate, to subcordate basal leaves, narrow praemorse rhizomes, giving rise to slender single stems topped with strict corymbs bearing few, small heads. Some specimens (Virginia and North Carolina) have sparse short stiff white hairs on the veins of the undersides of basal leaves and leaf tufts. This is not evident on the type as the counterparts are entirely pasted down. The habitat of var. *gracilis* appears to be calcareous sedgy meadows. It has a definite range, as stated by Fernald (1950).

Immature and depauperate herbarium specimens of *Senecio aureus* var. *aureus* (under which name I include all other varieties of this species *sensu* Fernald, 1950) may be superficially confused with var. *gracilis*, which may account for recent tendencies to submerge the latter. The habitat of the typical variety generally differs: bogs, swamps, and wooded areas near water. It may occasionally invade calcareous sites but seems to prefer acidic or neutral habitats.

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LITERATURE CITED

BARKLEY, T. M. 1962. A revision of *Senecio aureus* Linn. and allied species. Trans. Kans. Acad. Sci. **65:** 318–408.

_____. 1978. *Senecio*. No. Am. Fl. Ser. II, pt. **10:** 50–139.

EWAN, J. 1979. Introduction to reprint edition of Pursh, Flora America Septentrionalis, J. Cramer, Braunschweig.

FERNALD, M. L. 1950. Gray's manual of botany, 8th. Ed. New York.

LYSAGHT, A. M. 1971. Joseph Banks in Newfoundland and Labrador, 1766. London.

PURSH, F. 1814. Flora America Septentrionalis. London.

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RANGE EXTENSIONS OF VASCULAR PLANTS FROM THE SEWARD PENINSULA, NORTHWEST ALASKA

By Sylvia Kelso[1]

As a barrier, filter, or avenue of migration, the concept of a North American-Asiatic land connection linking Siberia to Alaska through the Bering and Chukchi seas has been the subject of much interest since it was first speculated upon by Wallace in 1876. Enough data have accumulated now from the disciplines of biology, geology, and anthropology, among others, to accept unequivocally that such a connection did exist through not only one but several periods in the past, the most recent ending some 12,000 years ago (c.f. Hopkins, 1979). The vast area under the influence of the land bridge, known as Beringia, stretches from the Kolyma River in Siberia to the MacKenzie Delta in Canada (Yurtsev, 1972). Today, many biotic distribution patterns in this region have their origins in aspects of paleogeography (c.f. Kurten, 1966; Krassilov, 1976; Sher, 1976). As more becomes known about contemporary patterns of biotic distribution, more can be explained about the geography of times past. Concurrently, as more is learned about historical changes, more can be understood about the patterns of today.

The location of Alaska's Seward Peninsula in the heart of the North American half of Beringia (Figure 1) has long stirred the interest of phytogeographers in the floristics of that region. From the early 19th century and the work of the botanist Chamisso who voyaged through the Bering Strait with the explorer Otto von Kotzebue, to the present, numerous collections have been made along the coast of the peninsula (c.f. Flett, 1901; Porsild, 1938; Hultén, 1968; Young, 1971; Racine, 1979) that was easily accessible by sea or more recently, by air. Unfortunately, however, due to its size and general inaccessibility from lack of a road system, the interior of the Seward Peninsula, which may be a critical area for our understanding of the American sector of Beringia, was neglected and remained generally blank except for sporadic collections from a few isolated points. Road systems now extend from Nome to the northwest, north, and east. This has made much of the interior more

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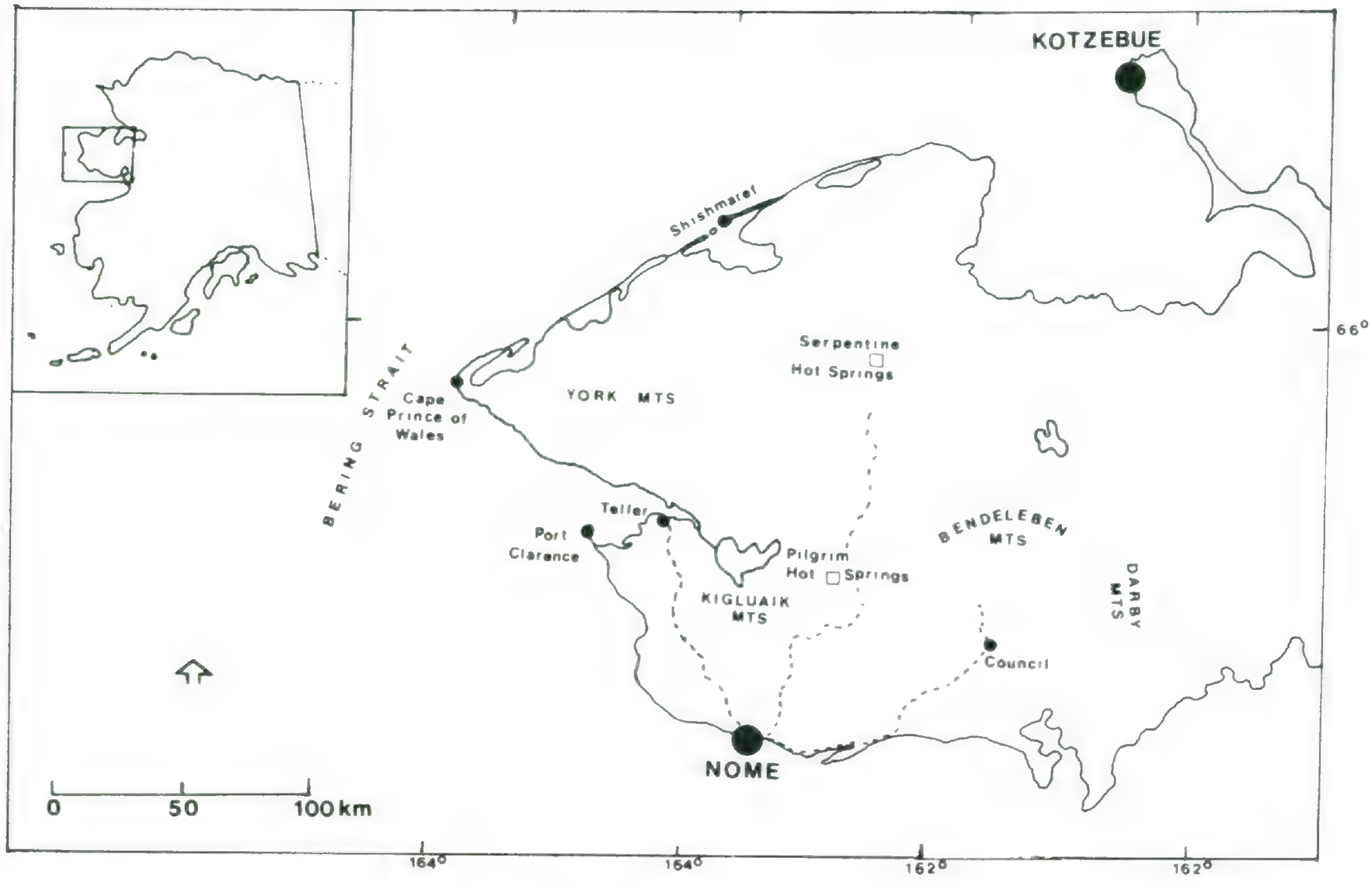

Figure 1. Seward Peninsula, Alaska.

accessible and blank areas can begin to be filled. During the field seasons of 1981 and 1982, the author had the opportunity to make collections in previously unexplored portions of the Seward Peninsula. This paper notes important floristic discoveries for the region.

The Seward Peninsula is generally mountainous and includes the York, Kigluaik, Darby, and Bendeleben Ranges (Figure 1). These offer rugged alpine terrain in contrast to the rolling lowlands and the opportunity for a strong connection to the mountain chains of Northeast Asia and to the Brooks and Alaska Ranges in Alaska. Much of the area was subject only to local alpine glaciation or none at all during the Pleistocene (Sainsbury, 1967). The Kigluaik Mts. have only recently emerged from glaciation and contain a relict glacier in the vicinity of Mt. Osborne (A.B. Till, U.S. Geologic Survey, pers. comm.). In contrast to a periglacial environment, anomolously warm habitats created by geothermal activity can be seen at Serpentine and Pilgrim Hot Springs.

Botanical exploration of the interior of the Seward Peninsula is only just now beginning. As the alpine regions become better known, puzzling floristic gaps may well be filled. The following taxa have recently been discovered on the Seward Peninsula and constitute noteworthy range extensions for the area (c.f. Hultén, 1968). Specimens cited here are deposited at the University of Alaska Museum Herbarium, Fairbanks (ALA).

GRAMINEAE

Alopecurus aequalis Sobol.

BENDELEBEN QUAD.[1]: Mile 60, Kougarok Rd, Central Seward Peninsula. In the margins of an ephemeral pond, 70 msm. *Kelso 82-219* 15 August 1982

This is a circumpolar taxon that was believed to have a notable gap in its distribution between the Chukchi and Seward Peninsulas (Figure 2). Kozhevnikov (1981) and Yurtsev et al. (1979) have now reported it from the interior of the Chukchi Peninsula and this discovery on the Alaska side of the Bering Strait shows the gap does not exist.

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[1]Note: The term "Quad" refers to the U.S. Geologic Survey topographic map at the scale of 1:250,000. These are used in lieu of county divisions which do not exist in Alaska.

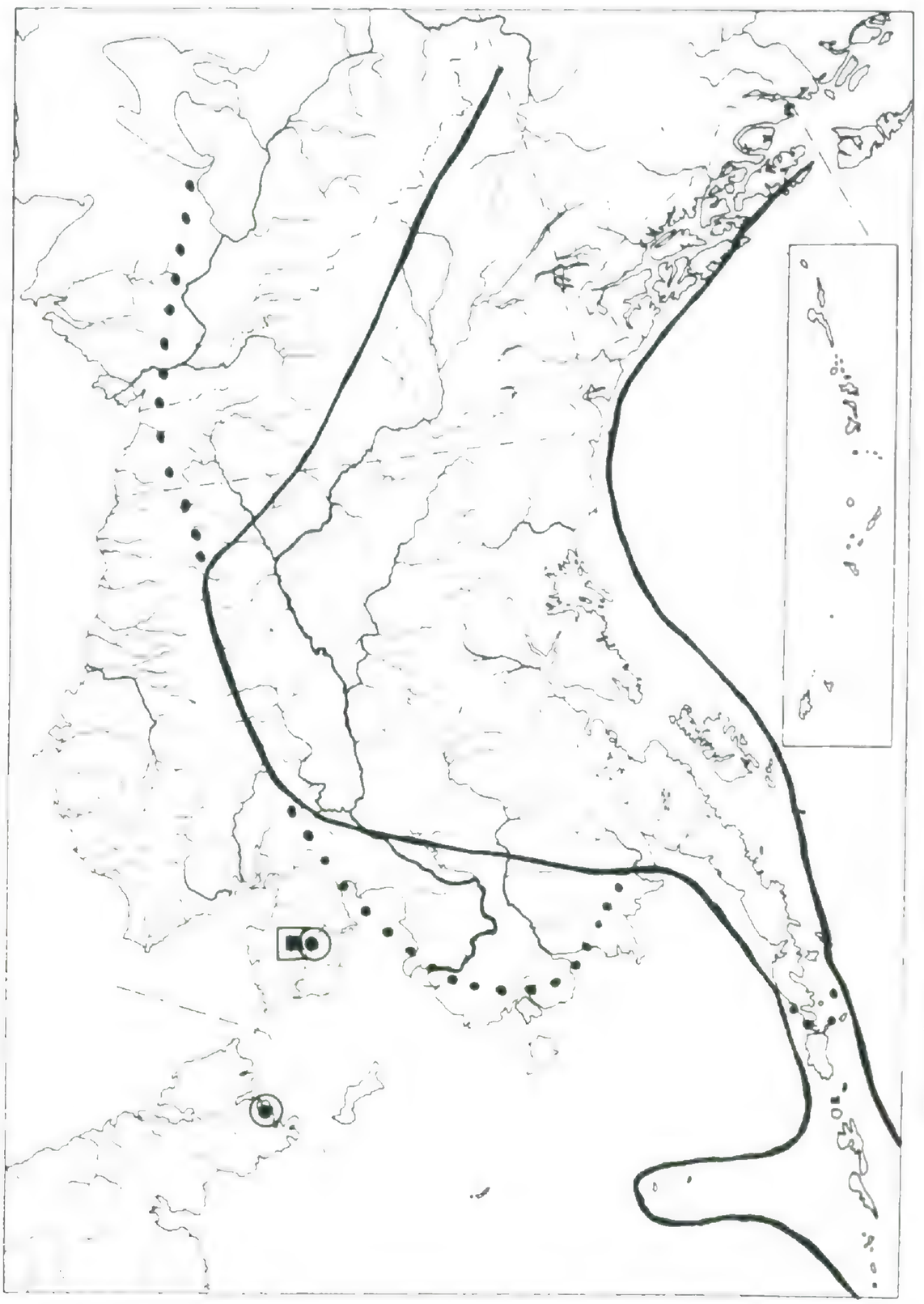

Figure 2. Ranges of *Alopecurus aequalis* (solid line, squares) and *Agrostis scabra* (dotted line, circles)

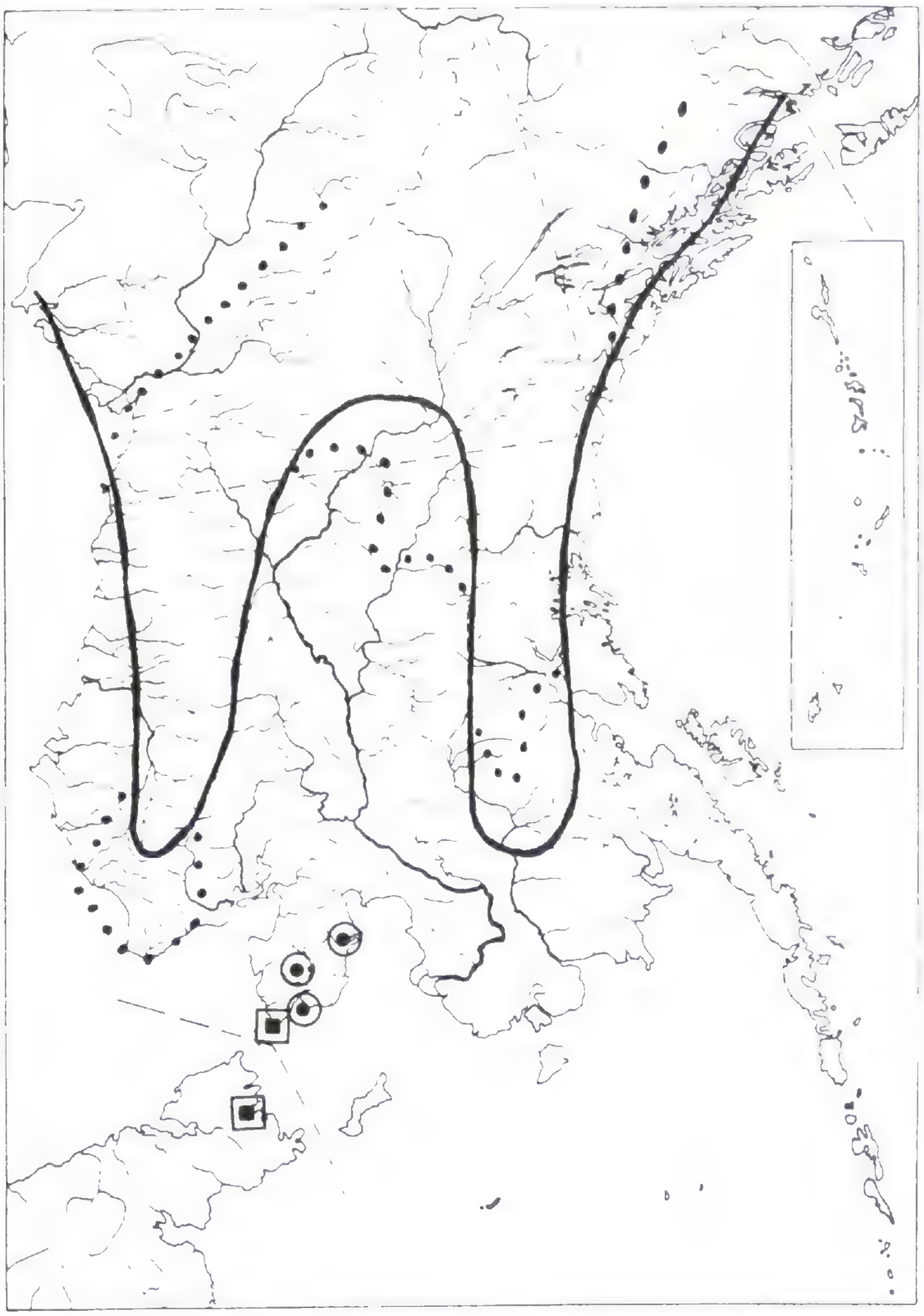

Figure 3. Ranges of *Carex bicolor* (solid line, squares) and *Crepis nana* (dotted line, circles)

Agrostis scabra Willd.

BENDELEBEN QUAD.: Pilgrim Hot Springs, Central Seward Peninsula, 70 msm. *Kelso 82-133* 20 July 1982

This is a boreal taxon common in open or disturbed areas throughout the coniferous forest region of North America east to Newfoundland, with isolated occurrences in Chukotka (Figure 2). This location at Pilgrim Hot Springs (c.f. *C.H. Racine #439* from Serpentine Hot Springs at ALA) extends the range northwestward.

CYPERACEAE

Carex bicolor All.

TELLER QUAD.: Cape Prince of Wales. Shore of Lopp Lagoon, in sandy gravel near the reindeer corral, 0 msm. *Kelso 82-151* 26 July 1982

Carex bicolor is an arctic-alpine taxon found in Alaska at higher elevations in the Brooks and Alaska Ranges with outliers in Chukotka (Figure 3). This discovery at Cape Prince of Wales is the first on the Seward Peninsula and extends the American range considerably to the westward. The sea level habitat exemplifies the strong alpine connections common on the Seward Peninsula where habitat and severe climatic conditions create alpine-type environments at very low elevations.

COMPOSITAE

Crepis nana Richards.

BENDELEBEN QUAD.: Kougarok Rd., Mile 59, in riparian gravel of the Pilgrim River, 70 msm. *Kelso 82-201* 12 August 1982

Crepis nana is an arctic-alpine plant known from Asia and North America. It has a wide range from Labrador to Central Siberia, but the distribution has been mapped as sporadic. On the Seward Peninsula it is known from Port Clarence on the coast and this occurrence in the interior is not surprising (Figure 3).

PRIMULACEAE

Androsace alaskana Cov. and Standl.

BENDELEBEN QUAD.: Kougarok Rd, Mile 51. On limestone outcrop, in sandy crevices, 75 msm. *Kelso 82-223* 17 August 1982

This is a North American taxon of relatively narrow distribution throughout the Alaska Peninsula to the Wrangell-St. Elias Moun-

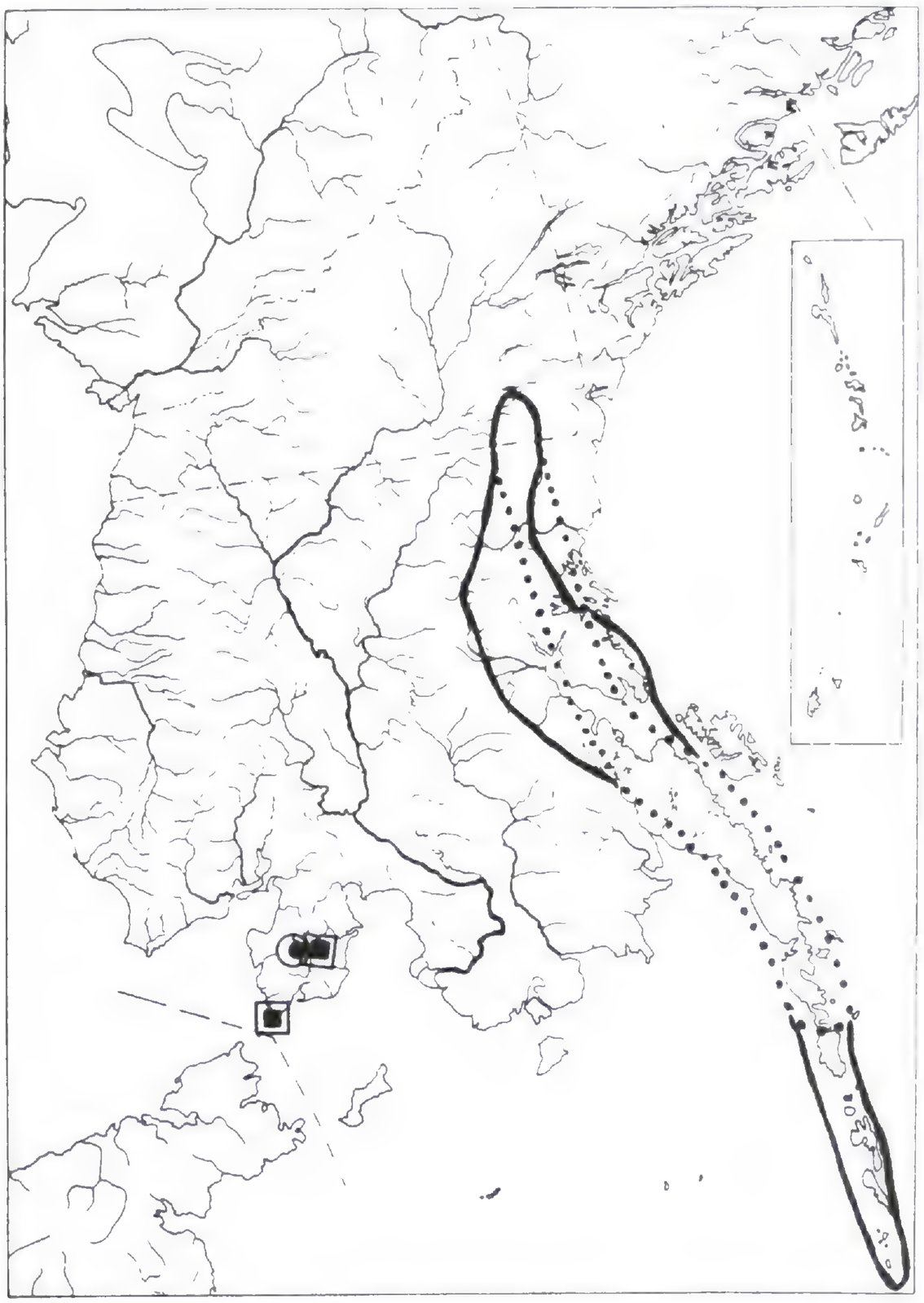

Figure 4. Ranges of *Aphragmus eschscholtzianus* (solid line, squares) and *Androsace alaskana* (dotted line, circles)

tains. Its presence on the Seward Peninsula, widely disjunct from the rest of the range, is quite remarkable (Figure 4).

CRUCIFERAE

Aphragmus eschscholtzianus Andrz.

TELLER QUAD.: Cape Prince of Wales. On wet solifluction soil, steep north-facing limestone slope, 80 msm. *Kelso 81-352* 27 July 1981

Aphragmus eschscholtzianus has a very similar distribution pattern to that of *Androsace alaskana*, reaching from the Aleutians into the Wrangell St. Elias region. Similarly, this discovery is a disjunct outlier on the Seward Peninsula; the plant has also been found once in the Kigluaik Mts. and is now known from the western tip of the peninsula as well (Figure 4).

REFERENCES

FLETT, J. B. 1901. Notes on the flora around Nome City. Plant World **(4)**: 67–68.

HOPKINS, D. M. 1979. Landscape and climate of Beringia during late Pleistocene and Holocene times. pp. 15–41. *In:* W. S. Laughlin and A. B. Harper (eds.) The First Americans: Origins, Affinities and Adaptations. Gustav Fischer, N.Y.

HULTÉN, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, California.

KOZHEVNIKOV, Y. 1981. Catalogus plantarum vascularum terrae tschuktschorum. Novosti Systematiki Vysshikh Rastenii **18**: 229–248.

KRASSILOV, V. A. 1976. The role of Bering land connections in the formation of the Cenozoic floras of east Asia and North America. *In:* Beringia in Cenozoic. "Report of the All-Union Symposium on the Bering Land Bridge, Khabarovsk, 1973. pp. 129–134.

KURTEN, B. 1966. Pleistocene mammals and the Bering Bridge. Comm. Biol. Soc. Fennica **29**: 1–7.

PORSILD, A. E. 1938. Flora of Little Diomede Island in Bering Strait. Transactions of the Royal Society of Canada ser. 3, sect. **5**(32): 21–38.

RACINE, C. H. 1979. Floristic and vegetational studies. *In:* H. R. Melchior (ed.) Biological Survey of the Bering Land Bridge National Monument. Revised final report to the National Park Service, Alaska Cooperative Park Studies, University of Alaska, Fairbanks.

SAINSBURY, C. L. 1967. Upper Pleistocene features in the Bering Strait area. U.S. Geologic Survey Professional Paper, **575**-D: 203–213.

SHER, A. V. 1976. The role of Beringian land in the development of holarctic mammalian faunas in the late Cenozoic. pp. 227–241. *In:* "Beringia in Cenozoic." Report of the All-Union Symposium on the Bering Land Bridge, Khabarovsk, 1973.

WALLACE, H. R. 1876. The geographical distribution of animals. Harper, N.Y.

YOUNG, S. B. 1971. The vascular flora of St. Lawrence Island with special reference to floristic zonation in the arctic region. Contr. Gray Herb. **201**: 11–115.

YURTSEV, B. A. 1972. Phytogeography of northeastern Asia and the problem of transsberingian floristic interrelations. pp. 19–54. *In:* A. Graham (ed.) Floristics and paleofloristics of Asia and eastern North America. Elsevier Publishing Co., Amsterdam.

YURTSEV, B. A., V. V. PETROVKSY, A. A. KOROBKOV, T. M. KOROLEVE, & V. Y. KAAZHIIVIN. 1979. A review of the geographic distribution of vascular plants of the Chukotka tundra. Bull. Mosk. O-Va Ispyt. Prirody. Otd. Biol. **84**(5): 111–120; **84**(6): 74–83.

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JAMAICAN BLUE-GREEN ALGAE COLLECTIONS OF J. C. STRICKLAND[1]

W. JOHN HAYDEN

Professor John C. Strickland (1915-1980) devoted much of his life to teaching biology, botany, and phycology at the University of Richmond. Throughout his academic career he maintained a keen interest in the Myxophyceae, or blue-green algae, studying their culture, cytology, and taxonomy (Drouet & Strickland, 1942; Strickland, 1940, 1946). Most of his collections of these and other algae were made in Virginia and are housed in the herbarium maintained by the Department of Biology, University of Richmond. However, he also made four trips to Jamaica in the years 1966-1971 before his health deteriorated to the extent that field work, and even processing of specimens, became impossible. Recently, Dr. Strickland's Jamaican collections of Myxophyceae have been identified through the kindness and diligence of Dr. Francis Drouet of the Academy of Natural Sciences, Philadelphia. This brief note provides an overview of Dr. Strickland's Jamaican collections, which constitute a significant contribution to the cryptogamic flora of the island.

The following list consists of 154 records of 17 species from nine parishes of Jamaica. With the exception of *Entophysalis deusta,* all the records are from freshwater or terrestrial habitats. Taxonomy and nomenclature follow Drouet and Daily (1956) and Drouet (1968, 1973, 1978, 1981). Habitat descriptions merely summarize label data; actual ecological ranges in Jamaica for these algae may be greater than indicated. To save space, locality data are limited to parish. Mixed collections are commonplace with these microorganisms. Collection numbers listed for each species include every gathering in which that species is present, regardless of its relative abundance in mixed collections. The collection numbers also provide some indication of abundance. Complete sets of specimens have been deposited in IJ and PH, as well as in the Department of Biology, University of Richmond.

[1]Publication supported in part by the Faculty Research Committee, University of Richmond.

Anabaina licheniformis Bory; over bare soil, roadside ditches. Portland: *2016*. St. Mary: *1994*.

Anacystis montana (Lightf.) Dr. & Daily; moist limestone rock faces. Manchester: *2011*. Portland: *1959*. St. Mary: *1987*.

Calothrix parietina (Näg.) Thur.; submerged or exposed limestone rocks. St. Catherine: *2074, 2075, 2079, 2082*. St. Mary: *2092*.

Coccochloris stagnina Spreng.; moist limestone rock faces. Clarendon: *2038*. Portland: *1959, 2019*. St. Andrew: *2025*. St. Ann: *2000*. St. Mary: *1980, 1983, 1995*. St. Thomas: *1975*.

Entophysalis deusta (Menegh.) Dr. & Daily; salt pond beach. St. Thomas: *1978*.

Microcoleus lyngbyaceus (Kütz) Crouan; floating or submerged in standing water. Clarendon: *2074*. St. Catherine: *2077*.

Microcoleus vaginatus (Vauch.) Gom.; on bare soil. St. Catherine: *2078*.

Nostoc commune Vauch.; standing water, moist soil, among mosses, moist rocks. Clarendon: *2036, 2048, 2053*. Manchester: *2012*. Portland: *2017, 2018, 2019, 2021, 2067*. St. Andrew: *1963, 2022*. St. Ann: *2006, 2064, 2065*. St. Catherine: *2073*. St. Mary: *1983, 1993*. St. Thomas: *1975*.

Oscillatoria principes (Vauch.) Gom.; floating in pool. St. Catherine: *2077*.

Oscillatoria retzii Ag.; wet soil and rock crevices. Clarendon: *2046, 2049*. St. Mary: *2060, 2071*. St. Thomas: *1976*.

Palmogloea protuberans (Sm. & Saw.) Kütz; limestone cliff faces. St. Ann: *2003, 2004*.

Porphyrosiphon notarisii (Menegh.) Kütz; on exposed rocks and on submerged debris in hot springs at Bath (water temperature 45° C). Portland: *1957, 2060a, 2060b*. St. Thomas: *1968, 1979*.

Schizothrix calcicola (Ag.) Gom.; submerged or exposed limestone rocks, over wet mud. Clarendon: *2034, 2037*. St. Andrew: *2023*. St. Ann: *2000, 2084*. St. Catherine: *2075*. St. Mary: *1995, 2069, 2071, 2082*.

Schizothrix friesii (Ag.) Gom.; over moist soil. St. Mary: *1991*.

Schizothrix rubella Gom.; over moist soil, moist rocks. Clarendon: *2037, 2057*. Portland: *2067*. St. Andrew: *2013, 2014*. St. Mary: *2081, 2088*. St. Thomas: *1965*.

Schizothrix tenerrima (Gom.) Dr.; over moist soil, moist rocks. Clarendon: *2043*. Portland: *2067*.

Scytonema hofmannii Ag.; nearly ubiquitous on moist surfaces, especially rocks, but also soil, tree trunks, and among mosses and lichens. Clarendon: *2031, 2032, 2033, 2034, 2035, 2036, 2041, 2043, 2044, 2045, 2049, 2051, 2052, 2057, 2058*. Manchester: *2010, 2011*. Portland: *1956, 1958, 1959, 1961, 1962, 1974, 2060b, 2061, 2067*. St. Andrew: *1963, 1964, 2013b, 2024, 2026, 2027, 2027a*. St. Ann: *1999, 2000, 2001, 2002, 2003, 2004, 2066, 2068, 2080, 2083, 2085, 2086, 2087*. St. Catherine: *2028, 2076*. St. Elizabeth: *2059*. St. Mary: *1980, 1981, 1982, 1983, 1984, 1985, 1986, 1988, 1990, 1991, 1992, 1995, 1996, 1997, 1998, 2088, 2089, 2090, 2093*. St. Thomas: *1965, 1966, 1967, 1969, 1970, 1971, 1972, 1973, 1975, 1977*.

Stigonema ocellatum (Dillw.) Thur.; on roadside bank. Portland: *2063*.

LITERATURE CITED

DROUET, F. 1968. Revision of the classification of the Oscillatoriaceae. Monogr. Acad. Nat. Sci., Philadelphia **16:** 1–341.

_____. 1973. Revision of the Nostocaceae with cylindrical trichomes. Hafner Press, New York.

_____. 1978. Revision of the Nostocaceae with constricted trichomes. Nova Hedwigia **57** (Beihefte): 1–258.

_____. 1981. Revision of the Stigonemataceae. Nova Hedwigia **66** (Beihefte): 1–221.

_____., & W. DAILY. 1956. Revision of the coccoid Myxophyceae. Butler Univ. Bot. Studies **10:** 1–218.

_____., & J. C. STRICKLAND. 1942. Arthrospira Khannae. *In:* F. Drouet. Studies in Myxophyceae I. Field Mus. Nat. Hist. Bot. Ser. **20:** 141.

STRICKLAND, J. C. 1940. The Oscillatoriaceae of Virginia. Amer. J. Bot. **27:** 628–633.

_____. 1946. The culture of certain marine algae. Science **103:** 112–113.

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NEW ENGLAND NOTES:

DISTRIBUTION OF THREE RARE PLANTS ON ISLANDS IN MACHIAS BAY, MAINE

ALAN J. LEWIS

A floristic survey of twelve islands in Machias Bay, Maine (44° 34′ – 44° 39′N; 67° 14′ – 67° 25′W) was conducted during 1979, '80, and '82. All islands were visited twice a month during May through September of each year. Of the species found, *Iris Hookeri* Penny. (Beachead Iris), *Sedum Rosea* (L.) Scop. (Roseroot), and Primula laurentiana Fern. (Bird's-eye Primrose) are listed as being at the southern limit of their range and rare in New England (Gawler, 1981; Olday, 1982). The results of this survey indicate that the species have become established at previously undiscovered sites and have probably become extinct at some reported stations (Table 1).

Populations of *Iris Hookeri* were well established and reproductive on the islands. Individuals were usually found growing in clumps distributed throughout low grassland, in bare humus around rock outcrops, or on beach sand or gravel deposits above the intertidal zone. Populations of *Sedum Rosea* were generally vigorous, reproductive and comprised of numerous individuals growing on rock outcrops on the margins of the islands. There were usually no associated species growing with *Sedum*, a fact which can probably be attributed to the rigor of the wind-swept habitat it occupies, the salt spray it often receives, and the paucity of soil in the crevices where it roots. Drury (1980), in his discussion of plant rarity, noted that "the range of some species is restricted to isolated localities yet they occur in large numbers at each locality." *Sedum Rosea* and *Iris Hookeri* are two species which exhibit this type of distribution in Maine.

The most significant discovery on any of the islands sampled was the population of *Primula laurentiana* on North (Big) Scabby Island. The southern section of the island rises sharply to a 93′ high dome and then falls off abruptly to an extended plateau which comprises approximately two-thirds of the island. *Primula laurentiana* grows profusely over an area about one hectare in size on the plateau. The average density in five randomly thrown quarter meter

quadrats was 18 plants/quadrat. The presence of pools and rock outcrops prohibits growth over the entire hectare, but a conservative estimate is that the population on this island contains over 100,000 individuals. Individuals in the population were vigorous and producing seed and vegetative offshoots. During July, 1982 numerous seedlings, as well as post-reproductive adults, were observed.

Another population of *Primula laurentiana*, composed of 23 individuals, was found on Ram Island in 1980. The plants were growing in sand and gravel-filled crevices around the edge of a brackish pool on the south-eastern side of the island. The island was not resurveyed until 1982. By then the population was extinct.

Although various hypotheses have been put forth to explain the distribution of *Primula laurentiana*, the question about controlling factors has not yet been resolved. Pike (1963) suggested that the species required an open habitat for survival and attributed its disappearance from Head Harbor Island to forest encroachment. The need for an open habitat is supported by the fact that the three islands in this study on which *P. laurentiana* occurred all lack forest cover. Pike (1963) also offered the opinion that the species distribution is controlled by a need for calcareous soil and cited the location of the plant near white-washed lighthouses as supporting evidence. No experimental test of this hypothesis has been conducted, however, and as Olday (1981) indicates, the plant occurs on six islands without lighthouses. Common habitat factors noted in this study were the restriction of *P. laurentiana* to areas whose surface was covered by fine stone fragments and which were generally lacking in organic matter and associated plant species. These observations suggest the alternative hypotheses that *P. laurentiana's* distribution may be controlled by a need for well-drained and aerated sites and/or by its inability to compete with other plant species.

ACKNOWLEDGMENTS

I thank Dr. Fred C. Olday for bringing the investigative area of rare plants in Maine to my attention and for his help in species identification. I am especially appreciative of the many hours of field and laboratory assistance provided by Ms. Deborah Webster-Pierce and for support provided by the University of Maine at Machias.

Table 1. Present distribution of *Iris Hookeri*, *Primula laurentiana*, and *Sedum Rosea* on islands in Machias Bay, Maine.

Species	Confirmed at Historic Site	Years Since Discovery	Unconfirmed at Historic Site	Previously Undiscovered Site
Iris Hookeri	North (Big) Libby (1960, G.)[a]	22		North (Inner) Double Headshot
	South (Little) Libby (1963, O.)	19		South (Outer) Double Headshot
	Ram (1980, O.)	2		Chance
	Scabby (no indication whether on North or South Island) (1980, O.)	2		North (Big) Scabby South (Little) Scabby
Primula laurentiana	South Libby (1911, G.)	71	North Libby (1960, G.)	Ram[b] North Scabby
Sedum Rosea	Old Man (1907, G.)	75		North Double Headshot
	Scabby (no indication whether on North or South Island) (1980, O.)	2		North Scabby South Scabby
	Ram (1980, O.)	2		
	South Double Headshot (1980, O.)	2		
	North Libby (1907, G.)	75		
	South Libby (1907, G.)	75		
	Foster (1960, G.)	22		

[a] Earliest published date of discovery, with investigator first listed by Gawler (G.), 1981 or Olday (O.), 1982.

[b] Population first discovered in 1980. Extinct on island by 1982.

LITERATURE CITED

DRURY, W. H. 1980. "Rare Species of Plants". Rhodora **82**: 3–48.

GAWLER, S., ed. 1981. "Rare Vascular Plants in Maine", A critical areas program report. Maine State Planning Office. 656 pp.

OLDAY, F. C. 1982. "Occurrence and Distribution of Four Species of Rare Vascular Plants Along the Coast of Eastern Maine". Maine State Planning Office, Report Number 77 (Draft copy). 49 pp.

PIKE, R. B. 1963. "Note on *Primula laurentiana* in Maine." Rhodora **65**: 286–288.

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NOTE ON *ADIANTUM PEDATUM* L. SSP. *CALDERI* CODY

SUSAN C. GAWLER

Adiantum pedatum L. ssp. *calderi* Cody, as described in the January 1983 issue of Rhodora (Cody, 1983) occurs at one Maine station as well as at the stations reported in Quebec, Newfoundland, Vermont, California, and Washington. The Maine station was discovered in 1977 by Jonathan Carter, researching plants of serpentine outcrops in Maine (Carter, 1979). Following Carter's directions, H. R. Tyler and I visited the site in September 1978.

We found a small population of *Adiantum pedatum* var. *aleuticum*, as it was called by Carter, growing on a serpentine outcrop on the northeast slope of Whitecap Mountain, Somerset County, Maine. Most of the mountain at this elevation (approximately 3100') is covered with dense spruce krummholz; the ferns grew in an isolated pocket which, presumably because of the serpentine outcrop, was basically unvegetated. The noticeably glaucous fronds were short and stiffly erect, with contracted pinnules. In stature, morphology, and ecology, these plants correspond to Cody's *Adiantum pedatum* ssp. *calderi* rather than to the variety to which they were originally referred.

Adiantum pedatum var. *aleuticum* (or, more correctly, ssp. *calderi*) has been listed as "threatened or endangered" in New England because it is known from only two sites in the region (Crow, et al., 1981). The one Maine site for this subspecies has been placed on the Main Register of Critical Areas (Critical Areas Program, 1981).

The original specimen from the Maine station (*Carter #513*, July 1977) was deposited at the herbarium of the University of New Hampshire (NHA). A second specimen (*Gawler & Tyler, s.n.*, 1 September 1978) has been deposited at the herbarium of the University of Maine at Orono (MAINE).

Cody's (1983) division of *Adiantum pedatum* into the subspecies *pedatum*, *calderi*, and *aleuticum* leaves ambiguous the position of the variety *subpumilum* W. H. Wagner, described in 1978. This extremely dwarfed variety, though known from horticulture, was only recently found in nature, on coastal cliffs of the Brooks Peninsula of Vancouver Island (Wagner & Boydston, 1978). As Wagner and Boydston point out, further study is needed to understand thoroughly the *Adiantum pedatum* complex.

LITERATURE CITED

CARTER, J. K. 1979. A floristic and phytogeographical analysis of selected serpentine sites in Maine. Master's Thesis, Department of Botany, University of New Hampshire, Durham, NH.

CODY, W. J. 1983. *Adiantum pedatum* ssp. *calderi*, a new subspecies in northeastern North America. Rhodora **85**: 93–96.

CRITICAL AREAS PROGRAM. 1981. Rare Vascular Plants of Maine. State Planning Office, Augusta, ME. 656 pp.

CROW, G. E., W. D. COUNTRYMAN, G. L. CHURCH, L. M. EASTMAN, C. B. HELLQUIST, L. J. MEHRHOFF, & I. M. STORKS. 1981. Rare and endangered vascular plant species in New England. Rhodora **83**: 259–299.

WAGNER, W. H., JR., & K. E. BOYDSTON. 1978. A dwarf coastal variety of Maidenhair fern, *Adiantum pedatum*. Can. J. Bot. **56**: 1726–1729.

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BOOK REVIEW:
AN ILLUSTRATED MOSS FLORA OF THE MARITIMES

BRENT D. MISHLER

Robert Ireland, of the National Museum of Natural Sciences in Ottawa, has produced a most excellent flora of the mosses of the Canadian Maritimes (New Brunswick, Nova Scotia, and Prince Edward Island). This work, the culmination of comprehensive herbarium studies and more than 15 years of field experience, has been carefully prepared with an eye toward maximal usefulness. This flora should certainly serve as a stimulus for increased study of the mosses of the Maritimes; it can equally serve as such for New England. Due to the geographic proximity and similar habitats in the two regions, almost all New England mosses can be identified with Ireland's flora, which perhaps surprisingly is the best single work yet available for the identification of New England mosses.

Bryophytes are commonly excluded these days from floristic and ecological studies of the "higher" plants. This unhappy circumstance is not merely a historical artifact; consider for example the treatments of bryophytes by Sullivant included in the early editions of Gray's Manual. Rather, knowledge of bryophytes of northeastern North America (especially the effective communication of knowledge to general botanists) has not kept pace with increasing knowledge of the tracheophytes. Thus the bryophytes have acquired the reputation of being difficult to identify. There really is no other good reason to separate and exclude the bryophytes from general studies of the land flora. Recent morphological and cytological work (some of which is reviewed by Scheirer, 1980, and Paolillo, 1981) has confirmed that the mosses in particular are close phylogenetic kin to the tracheophytes. Furthermore, bryophytes are subject to factors of distribution similar to those of the tracheophytes (Crum, 1972; Schuster, 1977). As Ireland states in his introduction (p. 9): "The distribution patterns of the Maritime mosses, like the mosses throughout North America, are nearly similar to those of the

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[1]IRELAND, ROBERT R. 1982. *Moss Flora of the Maritime Provinces*. 738 pp. National Museum of Natural Sciences Publications in Botany, No. 13. National Museums of Canada, Ottawa. Distributed by the University of Chicago Press. (Price: $25.00)

flowering plants. However, the small size of mosses allows them to survive in small niches....Therefore bryophytes are often better indicators of an ancient climate than flowering plants." Ireland's new flora, in conjunction with the recently published moss flora of eastern North America by Crum and Anderson (1981), provides not only a means of identification, but more importantly, a concise and useful picture of moss species as biological and ecological entities. These floras provide a foundation which should allow and encourage general botanists and ecologists to direct their attention to this fascinating group of plants.

The *Moss Flora of the Maritime Provinces* includes introductory material on distribution patterns, the structure and life cycle of mosses, collecting and herbarium techniques, past collectors of Maritime mosses, and hints on identification, methods of study, and the use of keys. There is a single bracketed key to genera, with 198 leads, which is made easier to use by headings restating characters, placed before major sections. This workable generic key is especially important because Crum and Anderson's flora does not include a generic key, making that flora less useful for non-specialists.

Ireland provides descriptions of 135 genera and 381 species; 398 full-page plates, handsome and accurate line drawings grouped at the end of each genus, illustrate most of the species. The species descriptions are short, giving only diagnostic characters, and include habitat, Maritime distribution, general range, chromosome numbers (when known), and miscellaneous remarks. The habitat descriptions and remarks are particularly valuable, reflecting the extensive field studies of the author. Many bryophytes are quite specific in their environmental requirements, making knowledge of habitat an important part of quick and positive identification. The species keys and descriptions work quite well, based on the specimens I ran through as a test. Ireland makes especially good use of pseudoparaphyllia as a character in several pleurocarpous genera (which is not surprising as he has made a special study of these characters: Ireland, 1971). The flora is completed by a rather long list of excluded taxa (previously reported from the Maritime Provinces but not confirmed by Ireland), a complete glossary (mostly taken from Crum, 1976, another compact flora that can be of use in New England), and an especially helpful 17 plates illustrating terms from the glossary.

Even though New England has been rather well collected, the lack of a modern, focused synthesis of its moss flora makes it impossible to state exactly how many New England species are also found in the Maritimes. It is clear however, that the great majority of species in our flora will satisfactorily key out in the *Moss Flora of the Maritime Provinces*. The exceptions are a few species of more southerly and westerly distribution in North America that reach the limits of their range in New England, for example *Sphagnum henryense, Fissidens obtusifolius, Hyophyla involuta, Desmatodon porteri,* and *Bryoandersonia illecebra*. Such species are usually uncommon locally, so are unlikely to confuse a Yankee user of Ireland's flora, but it will be necessary to consult the larger flora of Crum and Anderson (1981) on occasion.

The book is printed on good paper, sturdily bound in a sewn, cloth binding. I saw no typographical errors. There is a problem in the reproduction of some plates, really my only criticism of the book. Somewhere in the production process, perhaps in the photographic reduction of the plates, fine lines were lost in some plates, particularly in the habit drawings. Hopefully this problem can be corrected in later printings. In any case, these are only minor imperfections in what, considering the low price, must be one of the best botanical bargains in years.

I strongly recommend this flora for bryologists, general botanists and naturalists, ecologists, and libraries. If you could only own one book on the Maritime and New England mosses, this is the one. Dr. Ireland is to be congratulated upon bringing such an important and useful flora to completion.

LITERATURE CITED

Crum, H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. Journ. Hattori Bot. Lab. **35:** 269–298.

_____. 1976. Mosses of the Great Lakes forest. Rev. ed. University Herbarium, University of Michigan, Ann Arbor, Michigan.

_____., & L. E. Anderson. 1981. Mosses of Eastern North America. 2 volumes. Columbia University Press, New York.

Ireland, R. R. 1971. Moss pseudoparaphyllia. The Bryologist **74:** 312–330.

Paolillo, D. J., Jr. 1981. The swimming sperms of land plants. BioScience **31:** 367–373.

Scheirer, D. C. 1980. Differentiation of bryophyte conducting tissues: structure and histochemistry. Bull. Torrey Bot. Club **107:** 298–307.

SCHUSTER, R. M. 1977. Boreal Hepaticae: a manual of the liverworts of Minnesota and Adjacent Regions. J. Cramer, Vaduz. [reprint of The American Midland Naturalist **49** (1953): 257–684; **57** (1957): 203–256, 257–299; and **59** (1958): 257–332.]

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RUSSELL, EMILY W. B. 1983. Indian-set fires in the forests of the northeastern United States. Ecology **64**(1): 78–88.

Emily Russell presents the most thorough analysis to date of historical literature relating to Indian-set fires in the northeast. Her conclusion is that Indians did set fires locally, usually near their dwellings, but there is no evidence to support statements that Indians regularly burned forests over wide areas.

WHITNEY, GORDON G. & ROBERT E. MOELLER. 1982. An analysis of the vegetation of Mt. Cardigan, New Hampshire: a rocky, subalpine New England summit. Bull. Torrey Bot. Club **109**(2): 177–188

The authors present a quantitative analysis, using reciprocal ordination methods, of the vegetation at the summit of Mt. Cardigan. They recognize 2 environmental gradients—exposure and available soil moisture—as most important; and 3 major community types: dwarf evergreen shrub, deciduous shrub, and sub-alpine spruce-fir. They plot the population response patterns for 12 major species on the plot ordination.

Despite historical evidence of fires, they question whether the summit of Cardigan (and similar peaks) was ever completely forested at the very top, and feel that these wind-swept areas have served as refugia for arctic-alpine species.

PAILLET, FREDERICK L. 1982. The ecological significance of American chestnut (*Castanea dentata* (Marsh.)Borkh.) in the Holocene forests of Connecticut. Bull. Torrey Bot. Club **109**(4):457–473.

A marked increase in chestnut pollen makes this an excellent indicator for the boundary between the C_2 and C_3 climate zones (C_3 = 2000 years ago to present) inferred from New England pollen profile studies. An understanding of the modern ecology of chestnut, especially its reproductive strategy, is necessary in order to interpret correctly this pollen increase in relation to environmental conditions. The author presents working theories as a basis for future research.

BROWN, JAMES H. JR., CESAR A. CASTANEDA, & ROBINSON J. HINDLE. 1982. Floristic relationships and dynamics of hemlock

(Tsuga canadensis) communities in Rhode Island. Bull. Torrey Bot. Club **109**(3):385–391.

Hemlock stands probably represent some of the oldest and least disturbed forest communities in the state. In the absence of major disturbance, change occurs very slowly, and hemlock reinforces its dominant position in the stands.

SICCAMA, THOMAS G., MARGARET BLISS, & H. W. VOGELMAN. 1982. Decline of Red Spruce in the Green Mountains of Vermont. Bull. Torrey Bot. Club **109**(2):162–168.

The authors note the distinct decline of red spruce over a 15-year period, and present data to document this. The cause of the decline may be due to air pollution and resultant acid rain and heavy metal accumulation. Insects and fungal diseases also play a role.

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BOOKS RECEIVED

MOHLENBROCK, ROBERT H. 1982. The illustrated flora of Illinois. Flowering plants: basswoods to spurges. 234 pp. Carbondale, Illinois, Southern Illinois University Press. (price $22.95)

This is the 10th volume in a continuing series. Forty-two genera and 103 species are described, and keys are provided. Additional notes include synonymy, ecology, variations, range. Dot maps show Illinois distribution. A detailed line drawing by Mark William Mohlenbrock is provided for each species. These volumes are useful, far beyond the borders of Illinois.

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Vol. 85, No. 842, including pages 127–273, was issued April 21, 1983.

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Contrary to prior policy, Rhodora now requests that an *abstract* and a list of key words be supplied with all papers submitted except for very short articles and notes.

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Cover illustration

Trollius laxus Salisb. is very rare as it nears its northeastern limit in Connecticut. Some old records indicate that it has grown in parts of New Hampshire and Maine, so it may yet be found in appropriate habitat.

Original artwork by Tess Feltes, Illustrator.

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PLASTICITY EXPRESSED BY ROOT GROUND TISSUES OF RHIZOPHORA MANGLE L. (RED MANGROVE)

GEORGE S. ELLMORE, SUSAN C. LEE, AND NORTON H. NICKERSON

ABSTRACT

Roots of *Rhizophora* undergo striking changes in structure as they grow from the open air into the substrate. To test the hypothesis that darkness and oxygen deprivation are responsible for determining root form in the underground environment, above-ground roots were covered with plastic to limit gas exchange, and with foil to block out light. After 9 months growth, roots growing in darkness with restricted gas flow became swollen and branched, as did underground roots. However, in artificially covered roots, axis swelling was due to pith enlargement rather than elaboration of cortex lacunae, as occurs in underground roots. Thus, root plasticity is expressed via a different mechanism when roots are in darkness and deprived of O_2 than when they are underground. Other factors, alone or in combination, must govern development of underground *Rhizophora* roots.

Key Words: Mangrove, *Rhizophora*, root anatomy

The Red Mangrove, *Rhizophora mangle* (Rhizophoraceae) is a widely distributed tropical tree, critical to shore stability along warmer coasts, such as that of south Florida (Craighead, 1971). Its ability to stabilize coastal areas is due to the growth of conspicuous aerial roots which penetrate the substrate. Under ground, a series of striking changes occurs (Gill & Tomlinson, 1977) as roots grow from a single axis into a mass of thin, soil-building lateral roots. The underground root mass of *Rhizophora* becomes so dense that an anaerobic peat often develops.

Gill and Tomlinson (1977) review the typological literature dealing with *Rhizophra* root structure. Their studies greatly improved our understanding of mangrove roots because they stressed the changeable nature of living roots rather than treating the topic

solely in terms of phenomenology. Thus, a single growing root tip of *Rhizophora* is now known to undergo drastic changes in organization and in the sort of tissue it produces during its life span.

How do field conditions induce such fundamental changes in root growth? As a root tip grows from open air into a substrate, ambient conditions important to plant growth change. Among other properties (see discussion), the subterranean environment is moist, dark, and hypoxic relative to open air. The study of root dynamics in *Rhizophora* by Gill and Tomlinson (1977) suggests that darkness and oxygen supply govern the changes in root growth which occur underground.

In this study, we test the notion that darkness and/or oxygen deprivation are responsible for the characteristic growth form of underground mangrove roots. Attempts are made to simulate underground conditions around root tips which are still above ground (aerial). Aerial tips were deprived of oxygen or light, or both, and allowed to grow 9 months before being anatomically examined. We predicted that if low O_2 or darkness was in fact responsible for the underground growth form, our simulated conditions would produce an underground growth habit in spatially aerial roots. On the other hand, if no change in root form occurred, or if a form developed which differed from that of underground roots, then some other environmental condition(s) must influence growth of *Rhizophora* roots in the substrate.

MATERIALS AND METHODS

Experiments were performed on a natural stand of *Rhizophora* (2-4 meters tall) growing in oolitic sand on the tropic of Cancer. Hummingbird (Jewfish) Cay, seven miles west of Great Exuma, Bahamas, was the study site. On trees of the study population, aerial roots grew from 1-3 mm per day from July 1981-March 1982.

In an attempt to duplicate the dark, moist, subterranean conditions, tips of aerial roots were covered. Four sets of roots were studied (3-5 roots/set). Tips (20 cm) of one set were capped by polyethylene bags which were then filled with fresh water. This set of roots grew for 9 months with a restricted gas flow (due to the plastic covering), and with natural illumination (Fig. 1). Tips of another set were likewise covered with water-filled bags but in addition, each root tip was wrapped with aluminum foil to block out sunlight. This

set grew with restricted gas flow and in darkness (Fig. 1). Two other sets were untreated; one set was of aerial roots in the open air, the other was of underground roots (Fig. 1).

At the end of the 9-month growth period, root tips were collected, fixed in FAA, and sectioned for study. Only portions produced by the main root axis during these 9 months were sampled. Anatomy was studied using hand sections, stained in 0.1% toluidine blue and mounted in glycerine. Measurements were made using a calibrated ocular micrometer.

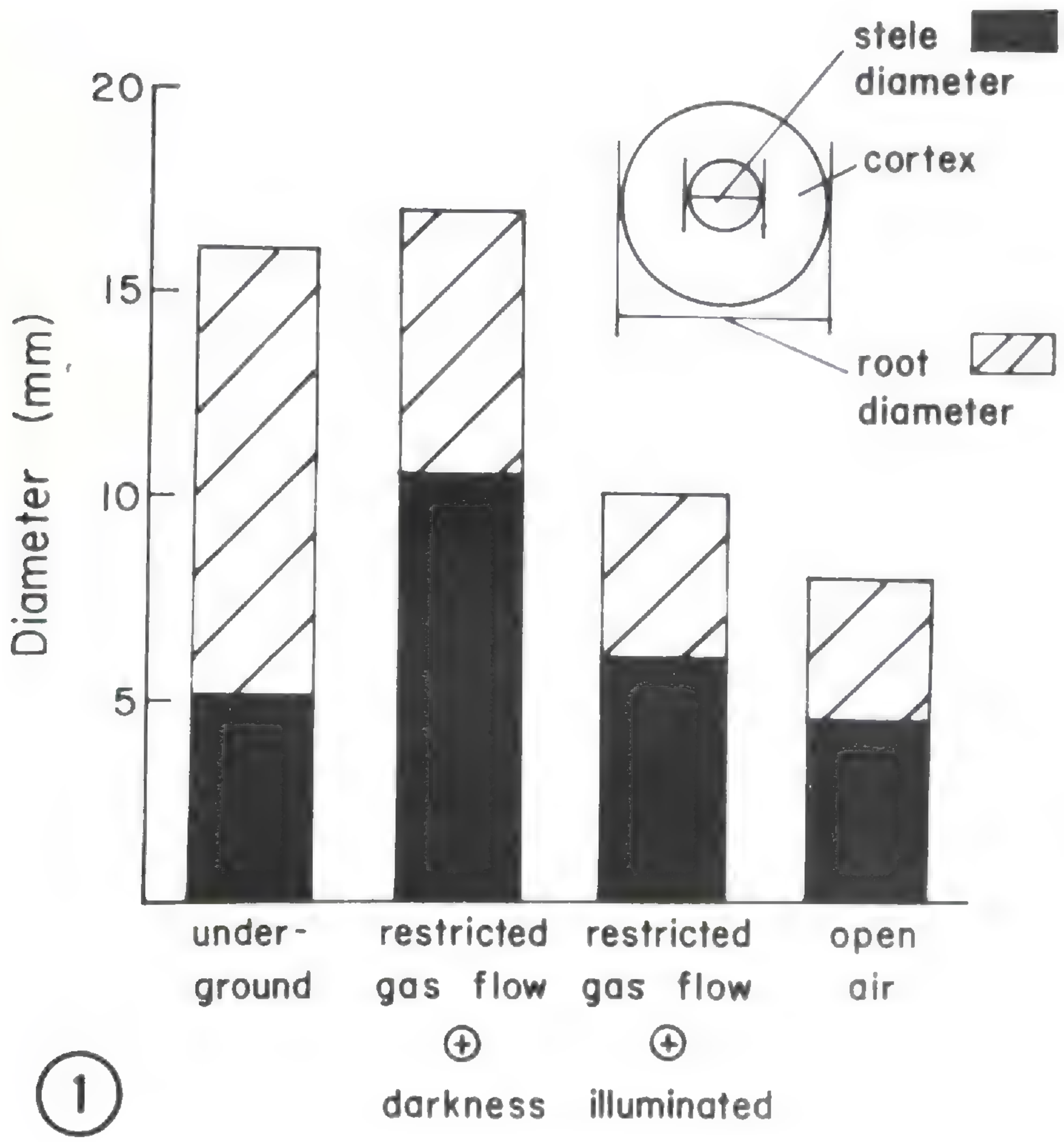


Figure 1. Cross sectional topography of *Rhizophora* roots grown 3 months under conditions indicated. Each bar represents an average derived from 3 to 5 samples. In all cases, standard error is less than 10% of the mean.

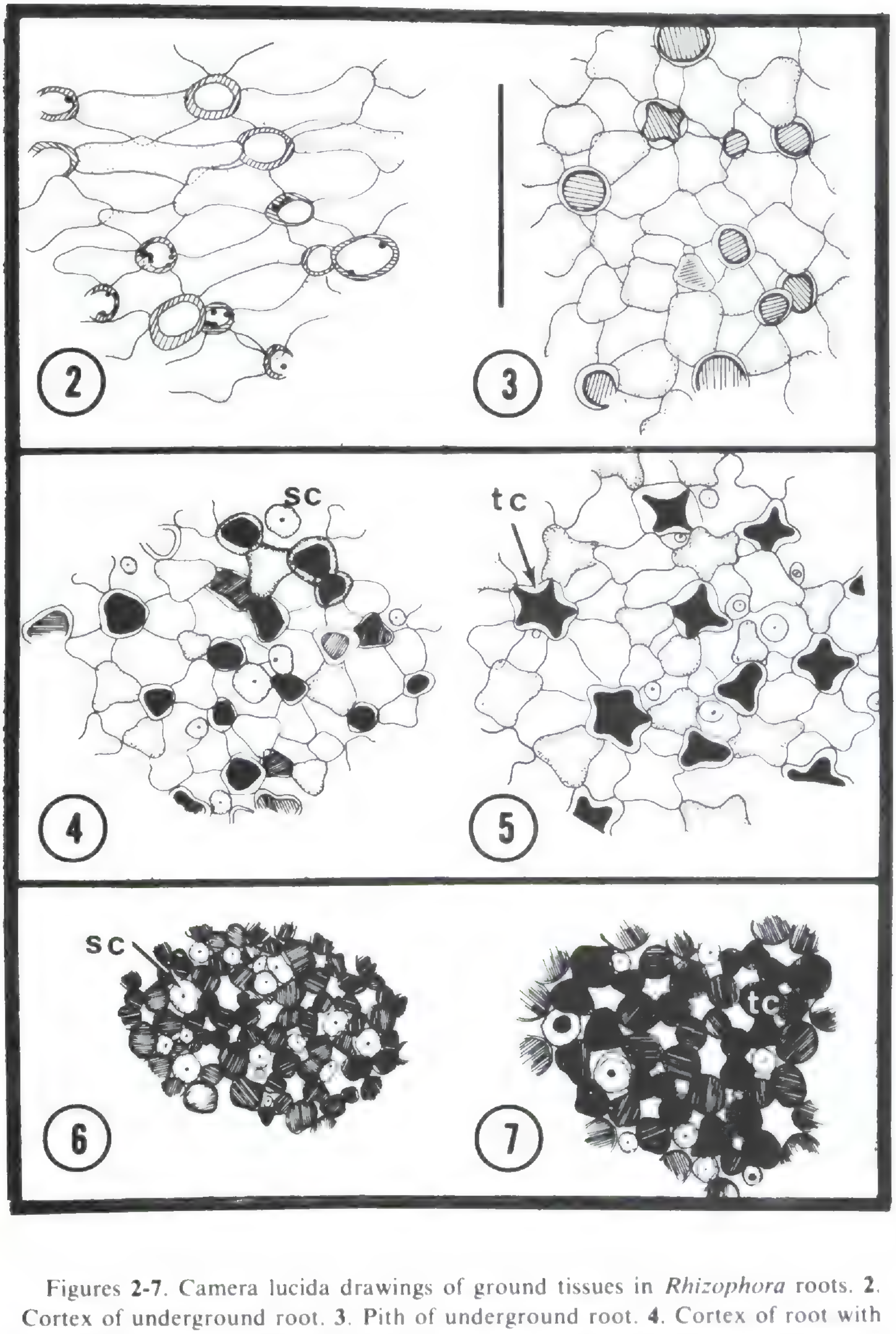
RESULTS

As previously shown by Gill and Tomlinson (1971; 1977) *Rhizophora* root structure changes dramatically as a root grows from the air into solid substrate, which at our study site is oolitic sand. Embedded in oolite, *Rhizophora* roots become twice as wide as aerial root axes (Fig. 1). Underground roots branch and show the diagnostic anatomy recently described (Gill & Tomlinson, 1977). Our attention is focused on the ground tissues (parenchyma of the cortex and pith). In the wide underground roots, 70% of the diameter is occupied by cortex, in contrast to 40% in the cortex of aerial roots (Fig. 1). Both cortex and pith are composed of vacuolate parenchyma cells (Figs. 2 and 3). Interspersed among them are cells filled with tannins and/or oil droplets. Tanniferous cells remain isodiametric, unlike the other parenchyma cells which stretch radially forming a system of intercellular spaces. In the cortex, these spaces average twice as wide (115 μm) as those in the pith (57 μm). The spaces are formed by radial elongation of cortex cells; cell-to-cell contact is maintained by conspicuous arm-like extensions of the cell wall (Fig. 2). Cells of the pith do not stretch as much as those of the cortex (Fig. 3), with the result that the gas spaces formed in the pith are smaller than those in the cortex. Trichosclereids occur only in the inner cortex.

Of the artificial growth conditions used, the combination of restricted gas flow and darkness produces roots that most resemble underground roots. Like underground roots, their diameter is over twice that of untreated (control) aerial roots (Fig. 1). However, it is the stele rather than the cortex which takes up over 60% of the root diameter (Fig. 1). In this case, intercellular spaces in the pith are on the average larger (70 μm) than those of the cortex (40 μm). Extended arms are more developed in pith parenchyma (Fig. 5) than in the cortex (Fig. 4). Trichosclereids occur in both pith and cortex. Untreated aerial roots have a narrow axis (Fig. 1). Small (19 μm) gas spaces occur in both the cortex and pith (Figs. 6 and 7). Trichosclereids are found throughout, as detailed by Gill and Tomlinson (1971).

DISCUSSION

The aim of our work was to determine the environmental cues responsbile for altering root development as the root tip grows form



Figures **2-7**. Camera lucida drawings of ground tissues in *Rhizophora* roots. **2**. Cortex of underground root. **3**. Pith of underground root. **4**. Cortex of root with restricted gas flow + darkness. **5**. Pith of root with restricted gas flow + darkness. **6**. Cortex of aerial root. **7**. Pith of aerial root. tc, tannin cell; sc, sclereid. Scale bar = 250 μm for all figures.

open air into the substrate. At first glance, roots covered for 9 months with plastic plus foil come to resemble underground axes. We were surprised to find, however, that this shift in morphology occurred via a different mechanism than any previously reported for *Rhizophora*. Like the underground root, the axis of roots wrapped in plastic and foil does swell and lateral roots develop. However, it is the *stelar* ground tissue (pith) which generates axis swelling in experimental roots (Figs. 1 and 5), unlike truly underground roots which swell via cortex enlargement (Fig. 1 and 2). This is a new example of the great plasticity of *Rhizophora* roots which allows them to contend with sudden shifts in ambient conditions. In terms of our intial hypothesis, it is clear that darkness and O_2 deprivation are not solely responsible for altering root form as apices grow under ground. If they were, roots with plastic and foil would have developed as do underground roots. Since they did not, other factors must influence development of underground roots.

Many aspects of the rhizosphere change as *Rhizophora* roots penetrate the substrate, and not all of them are obvious. Long considered have been differences in moisture, light, and O_2 levels between the aerial and underground environments. More recently, the significance to root biology of abrasion and pressure, buffered temperature regimes, soil microbes (Zuberer & Silver, 1979), and gas diffusion rates have been studied. These factors and others, such as altered nutrient availability, are known to strongly affect root development (Ellmore, 1982). For example, Drew, et al. (1979) found that a buildup in ethylene gas, rather than a depletion of oxygen, causes lacuna formation in flooded roots of *Zea*. This raises the possibility that underground *Rhizophora* roots may develop in response to increases in gases which would normally be carried away in a less confining environment. Interestingly, other aquatic plants such as *Ludwigia* (*Onagraceae*) develop lacunose tissue without producing large amounts of ethylene (Ellmore, 1981). *Rhizophora* resembles *Ludwigia* inasmuch as root lacunae develop by cell stretching rather than by the cell death seen in flooded *Zea*. Thus, it is not at all certain whether the ethylene requirement shown by *Zea* roots also applies to *Rhizophora*.

As stressed by Gill and Tomlinson (1977), the *Rhizophora* habitat is highly variable, and our results show that the stele as well as the cortex can respond to changing conditions. Knowledge of root biol-

ogy (Ellmore, 1982) has advanced to the point where a quantitative assessment of factors influencing *Rhizophora* root growth is needed. Future studies should first measure morphogenetically active components of the mangrove rhizosphere, then go on to test the effects of these components on mangrove root growth under controlled conditions. Such studies may go on to pave the way to controlling the destruction of mangroves which are essential to coastal stability throughout the tropics.

ACKNOWLEDGMENTS

This work was funded by a grant from the Hummingbird Cay Foundation, made to Tufts University.

LITERATURE CITED

Craighead, F. C. 1971. The trees of South Florida, vol. I. The natural environments and succession. University of Miami Press. Coral Gables.

Drew, M. C., M. B. Jackson, & S. Giffard. 1979. Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. Planta **147**: 83-88.

Ellmore, G. S. 1981. Root dimorphism in *Ludwigia peploides* (Onagraceae): structure and gas content of mature roots. Amer. J. Bot. **68**: 557-568.

———. 1982. The organization and plasticity of plant roots. Proc. Scanning Electron Microscopy **1982**, III: 1083-1102.

Gill, A. M. & P. B. Tomlinson. 1971. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 2. Growth and differentiation of aeriel roots. Biotropica **3**: 63-77.

———., & ———. 1977. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 4. The adult root system. Biotropica **9**: 145-155.

Zuberer, D. A., & W. S. Silver. 1979. N_2-fixation (acetylene reduction) and the microbial colonization of mangrove roots. New Phytol. **82**: 467-471.

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NOTES ON THE POLLINATION OF *SARRACENIA FLAVA* L. (SARRACENIACEAE) IN THE PIEDMONT PROVINCE OF NORTH CAROLINA

DONALD E. SCHNELL

ABSTRACT

Field studies were carried out on the pollination of *Sarracenia flava* L. during three flowering seasons in relict bogs of the piedmont region of North Carolina. Flowering occurs in latter April into early May, and the most systematic, common, and effective pollinators were found to be queens of *Bombus* spp. Smaller native bees and *Apis mellifera* are at best accidental or occasional secondary pollinators, mainly because of infrequency of effective flower visits and the small size of the insects relative to modes of flower entry and exit. *Sarcophaga sarraceniae* activity around flowers is very rare in this area and is not of any consequence in pollination. Various other aspects of the problem discussed in the literature over the years are reviewed critically, among them the question of protandry. The flowers were found not to be protandrous. Nectar and pollen output in these large, early spring flowers is prodigious, and nectar sugar concentration is 39%. Pollen was weighed and nectar output estimated. *Bombus* behavior while visiting a flower is described and the relative incidence of insect pollinator autogamy, geitonogamy, and xenogamy is discussed. Numbers of flowers visited in a foray, time in forays and time per flower are recorded.

Having made a few preliminary comments on the pollination of *Sarracenia flava* L. (Sarraceniaceae) in a previous paper (Schnell, 1978a), I sought to undertake more detailed observations in a different area of the plant's range. The 1978 paper commented on pollination of the species in the field in a coastal plain savanna of southeastern North Carolina and I concluded that *Bombus* spp. are probably the primary pollinators of *S. flava*. The present study was undertaken in relict seep slope sphagnum bogs of the piedmont province of the state, specifically in northern Iredell County. Here, observations could be made on an almost daily basis throughout the flowering season over several years.

The unique flower of the genus *Sarracenia* is well described in several standard references (Macfarlane, 1908; Russell, 1918; Uphof, 1936; McDaniel, 1971; Schnell & Kutt, 1973; Schnell, 1976) and will not be repeated in detail here. The flower's salient features are an essentially pendulous habit during anthesis with dehisced pollen collected in a floral compartment bounded by an umbraculate expansion of the style as the floor of the compartment, panduri-

form petals and upward projecting points of the umbraculate style along with lower portions of the sepals forming the lateral walls, and a large tuberculate ovary with hypogynously inserted bases of stamen fascicles (usually 5–6, each with 5 stamens), petals and sepals as the roof. The petals in *S. flava* are bright yellow, but in other species of the genus vary from shades of red to cream to pale yellow. During anthesis, flowers of *S. flava* have a strong, moderately unpleasant fragrance best described as "feline" (Schnell, 1978b). Near the close of anthesis, many flowers resume a more erect position similar to the bud stage, at which time petals are shed. Seed matures over summer in the ripening ovary. The green umbraculate style and sepals are retained during the entire summer.

MATERIALS AND METHODS

Field studies were done in three relict seep slope sphagnum bogs located in the piedmont province of North Carolina, specifically Iredell County ca. 18 km NNW of Statesville. These are small, partially open bogs located in farmland, the largest being about 0.5 hectare. Two of the bogs contain *Sarracenia flava* only; the largest also has a few plants of *S. purpurea*, with rare hybrids (*S.* × *catesbei*). All the bogs are in the Rocky Creek watershed, which has several more sphagnum bogs of lesser interest.

Studies were carried out during the flowering season of the years 1980–1982. Field observations were made during some part of nearly every day of anthesis for time periods ranging from two to four hours at differing times of the day. Two evening watches were carried out through dusk until complete darkness (2200 hours EDT). Observations were made in all weather from cool rain or drizzle, windy or still, to quiet, warm and sunny days. Observations for pollinator activity followed the criteria of noting systematic, purposeful, apparently learned effective working of a flower in such a way as to transfer pollen to stigmas (modified from Burr, 1979; and Faegri & van der Pijl, 1979).

Autogamy tests were carried out by gauze bagging twenty flower buds early in the season and removing covers after petals dropped. Selfing and intraspecific outcrossing had been done by me over the past twenty-five years during which I have been growing and studying the genus, and the species selfs and outcrosses freely with full seedset, there being no observed advantage of one method over the other as far as final viable seed size and quality are concerned.

Pollen output weights were done by brushing all pollen from the umbraculae of five bagged flowers after complete anther dehiscence, and weighing the quantitites on a Mettler H54AR balance (Mettler Instrument Corp., Box 100, Princeton, NJ 08540). This was done to gain some approximate idea of the range of maximum pollen output per flower.

Total nectar sugar content was estimated by collecting nectar drops in capillary glass tubes from around the bases of stamens where it aggregated. Collections were made from several dozen flowers, the nectar pooled, and then measured in an American Optical Corporation refractometer especially calibrated for sugar estimations.

Histologic sections were made and stained of the bracts, sepals, petals, ovary, and umbraculum of several flowers to determine extent and kind of gland distribution, standard histologic techniques being used. The stigma knob was examined with a dissecting microscope to clarify its gross morphology.

Insect pollen load was noted by capturing flower visitors and combing the pile of the dorsal and ventral abdomen, and scraping out corbicular contents. The pollen was then stained with lactol-phenol blue and characterized as *Sarracenia* or non-*Sarracenia*. Bee identifications are according to Mitchell (1960, 1962) and Heinrich (1979).

An attempt was made to discover the flower part source(s) of the unique flower frangrance of *S. flava* by dissecting and separating fresh flower parts (bracts, sepals, petals, style umbraculum, stamens, ovary and receptacle), placing these in sealed plastic bags or glass jars in full sunlight for an hour, and then noting the relative intensity of fragrance, if present, when uncapping.

Finally, since there is some confusion in the literature regarding possible dichogamy in the genus, I attempted to resolve the problem for this species in the study location as follows. A tight clone of several growth points having 15 flowers buds was selected in the study bog and was covered with close-mesh cage of window screen long before anthesis. The ground around the clump was thoroughly cleared of other growth to provide a tight fit of the cage bottom edge against the sphagnum and soil. Each bud was tagged and an identification number assigned. Day 1 of anthesis was defined as a completely opened flower with pendulous petals. Six flowers were hand-pollinated with their own pollen on day 1 for each flower, five

on day 2, and four on day 3, three days considered sufficient based on my experience with *Sarracenia* pollination, and since the question was one of protandry.

Ultra-violet photographic studies of flowers, a common part of pollination studies in many other genera and species in the past, were not done here in light of compelling arguments recently raised against their value, particularly regarding use of glass camera lenses, unbracketed exposures without grey scales, and apparently unwarranted assumptions on bee color vision which seems to involve the visible spectrum as well (see Kevan, 1978, 1979).

RESULTS

Gauze-bagged flowers of *Sarracenia flava* failed to set any seed in my experiments, dried and empty capsules resulting at season's end. However, in past efforts by me, flowers selfed by hand produced full seedset uniformly, as did outcrossing to flowers of the same and different clones within the species.

Pollen brushed from five bagged flowers at full dehiscence weighed as follows: 9.86, 19.17, 28.68, 47.57 and 48.55 mg. This gave an average of 30.77 mg and a median of 28.68 mg. There is little hard data in the literature on pollen output in various species and pollination syndromes; but the weights here, while variable and with relatively few samples, seem impressive for a single flower. In warm, sunny weather, all flowers had shed at least some pollen into the umbraculate cup on the first day of anthesis. In cooler, cloudy and wet weather, pollen dehiscence was often delayed a day into anthesis.

Nectar sugar content was found to be 39% by refractometer. *Sarracenia flava* nectar production was observed in undisturbed flowers growing in insect protected greenhouse as well as those caged and bagged in the field. The nectar grossly appears to be produced near the base of the ovary and collects as droplets among the stamen filament bases which act as wicks. Measuring droplet size (1.5–3.0 mm across) and calculating volumes from the five droplets among stamen fascicles at a moment of observation results in a flower volume of 4–10 μl. This is a "point in time" quantity since more nectar is soon formed as the droplets are removed or fall. The nectar itself is clear, colorless, pale yellow, and with a definite sweet taste having no aromatic component. The only time I ever saw nectar

pooled with pollen in umbraculae was in the case of flowers in the greenhouse, or bagged and caged in the field.

Histologic section examinations essentially confirm the results of Russell (1918). There are allurement glands over the central areas of the bracts, outside surfaces of sepals near their tips, and scattered lightly over the tips and pendulous portions of petals, but numerous near petal constrictions with no glands above that point. The complex glands in the bases of the pit canals coinciding with ovarian tubercles were most prominent over the basilar one third to half of the ovary. The glands found on other floral organs were simpler 1–3 celled surface glands. The ovarian glands are likely the source of nectar, considering the later's distribution as noted above, and the types and distribution of floral glands.

Examination of the stigma knobs located at each of the five points of the style umbraculum was of interest. The stigma knob appeared to consist of three zones, the combined structure measuring 1.5–2.0 mm in length: 1) a basilar, somewhat pyramidal tented portion of the umbraculum surface located at the point of the V-shaped cleft, the pyramidal base supporting 2) the short cylindrical column, on top of which is the 3) stigma tip or knob. The receptive stigma tip portion is villous, and this villous surface extends down the column abaxially a short distance as a V-shaped track. Adaxially, the villi occupy only a very small area at the very tip of the structure.

In the attempt to determine which parts of the flower were the source of fragrance, the odor strength was graded subjectively on a scale of 0 4+ when the containers were opened. Clearly, the strongest fragrance source resides in the petals (petal bases—3+, petal tips—4+), with the umbraculate portion of the style being 2—3+. Sepals were 2+, stamens and receptacles were 1+, with the ovary and basal style 0–1+, and bracts 0.

In the caged clone of 15 flowers pollinated by hand isogenously on specified days of anthesis, I found that 5 of 6 flowers pollinated on day one of anthesis had full seedset, 3 of 5 on day two, and 4 of 4 on day three of anthesis. Though numbers are small, these results indicate that the flowers of *Sarracenia flava* are not protandrous.

The peak flowering period for *Sarracenia flava* in the study area is a 3–4 week interval beginning the last week or two in April and extending into early May. The exact flowering peak is unpredictable

and seems to vary with weather factors, particularly temperature. The weather is capricious this time of year in piedmont North Carolina; often warm periods suddenly give way to cold, frosty nights and cool, cloudy days.

Night observations failed to disclose any insect activity from dusk into total darkness. Inspection of many flowers later in the evening failed to disclose *Sarracenia* flies resting in flowers. Dusk and nightflying moths do not appear to be pollinators. I did not notice increasing flower fragrance towards evening, but on the contrary found it stronger earlier in the day.

During daytime observation periods, various wasps were in the area often, especially mud daubers, but they did little more than work the sepals for external attractant nectar and they were never seen to enter the flower or even approach the petal or stigma. *Sarcophaga sarraceniae* were seen on and around flowers often, but seldom entered the floral chamber. On the rare occasions when they did enter a flower, the large size of the flower with its relatively open structure among *Sarracenia* flowers permitted these smaller insects to enter the opening between petals and umbrella projection without even touching the stigma knob, and they exited the same way. I would grant that occasional contact with the stigma knob might be achieved, and exiting flies were liberally dusted with pollen. But they were not sufficiently hirsute to maintain pollen loads in flight between flowers, and would at best seem to be accidental or secondary pollinators.

Small native bees identified as members of the families Megachilidae and Halicitidae also occasionally visited and entered flowers, but the comments applied to the *Sarracenia* fly above would be appropriate for these insects—too few visits and easy bypass of the stigma knob.

It was interesting to observe carpenter bees (*Xylocopa* spp.) who did no more with the flowers than did wasps but which flew small circuit patterns (several meters long by 1–2 meters wide) over the flowers, vigorously attempting to drive off any other insect visitors entering their flight patterns, thus exhibiting some evidence of territoriality.

During the three years of observation for this work, *Apis mellifera* was seen working *S. flava* flowers occasionally in one season. During the other two seasons, they were not seen near *Sarracenia*

flowers in the bogs at all in this area. Honeybees could also enter and leave an *S. flava* flower by avoiding the stigma knob completely, and during the few visits they did make in the one season they were seen to do so most of the time. Due to their larger size (cf. flies, smaller native bees, etc.), they tended to brush the stigma knob somewhat more frequently and probably effect pollination. Combings of pile (dorsal and ventral) and corbicular scrapings did disclose abundant *Sarracenia* pollen. There never was a massive, organized working of flowers in the bogs as is more typical for this bee species in a favorable area, and it is likely that the few visitors were scouts.

Various moths, butterflies, small beetles, and ants were sometimes seen on flowers' surfaces, but did not engage in pollinator activity.

Clearly, the one insect genus that stands out as a systematic pollinator of *S. flava* in this location is *Bombus*. Large individuals of *Bombus* (presumably queens this time of year and considering size of individuals) were very active all three years. Their structure, behavior, and size cause them to be ideal pollinators.

During the three study years, the accumulative *Bombus* spp. list is: *B. fraternus, B. affinis, B. perplexus, B. pennsylvanicus pennsylvanicus, B. nevadensis auricomus, B. impatiens,* and *B. bimaculatus*. Only a few of the species were present in all three observation seasons and there was considerable year to year frequency variation among them, but the genus as a whole was constant and abundant.

The general pattern of *Bombus* activity is as follows. An individual would fly into the bog along the periphery, following a relatively straight course to the nearest flowering clones. At a distance of about one meter or so from a clone, the straight flight would change to an irregular circling approach after which the bee would land on a sepal or pendulous portion of a petal. I noticed that individuals approached gauze-bagged flowers whose color was somewhat obscured by the gauze but from which strong fragrance was emanating. Also, I observed that some bees would approach rather tightly closed buds that were still green but from which the Sarracenia flava fragrance was becoming apparent. This bud approach was sometimes seen in bogs with many flower buds but before anthesis had occurred at all.

After landing on the petal, or sometimes the sepal, of the initial

flower of the foray, the bee would usually circumnavigate the flower beneath the sepals but external to the petals for one or more rounds. It would then enter the flower, upside down and head first, the dorsal pile always brushing directly and firmly over the stigma knob. Even smaller *Bombus* spp. had a snug fit between the two petal edges and stigma knob, and they often struggled to enter a flower. *Bombus* activity while in the flower can easily be observed by carefully lifting a petal; the bee goes about its activities ignoring the intrusion. Still inverted, the bee works the nectar droplets enmeshed among the stamen filament bases, collecting pollen on its ventral pile and in its corbiculae, and sometimes the dorsal pile would dip into the resevoir of dehisced pollen in the umbrella cup. While in the flower, the bee often vibrates its wings with a buzzing perceptably different from flight or balance seeking, and a cloud of pollen might fall from incompletely dehisced anthers. The bee would then often drop into the umbrella cup and move about in the pollen reservoir there.

If another bee approached an already occupied flower and attempted to enter, a small scuffle ensued following which it was almost always the interloper who was driven off.

Exit would be by one of three routes: 1) headfirst, inverted back over the stigma knob, thus brushing the stigma directly again; 2) lifting a petal hanging over a sway in the umbrella contour between stigma points, exiting upright and climbing the edge of the petal to the sepals; or 3) an intermediate exit in which the bee would brush the stigma knob somewhat sideways — but, due to its size, effectvely depositing pollen and partially lifting one edge of a petal which it would grasp and crawl to the sepals. Pile brushings (dorsal and ventral) and corbicular load examinations disclosed only *Sarracenia* pollen in abundance, even after flight to a second flower.

After crawling to the upper surfaces of the sepals, the bee would either stop to clean or would move promptly on to the next flower in a direct course (same clone or different), or sometimes would re-enter the flower just worked. Cleaning was never completely efective and pile and corbicular contents examinations disclosed abundant residual pollen. After cleaning, there was a liberal, irregular deposit of pollen on the sepal, and such "bee tracks" indicating a previous *Bombus* visit to that flower were distinctive and often observed on flowers while casually passing through a bog.

Flowers were open for five to ten days and each was worked many times over. I noticed a definite tendency to less bee activity on cooler, overcast, or windy days. I did not observe nectar robbing by *Bombus* puncturing sepals or by incomplete flower entry.

On different days of a season (1980), I observed how many flowers were worked (actually entered) per foray for a total of 46 forays. The fewest flowers worked was one, and the greatest 49, with an average and median of 8. This represents a marked skew and emphasizes that very large numbers of visits per foray were in the minority. These forays were counted early in anthesis and the longer ones were concurrent with shorter forays by other individuals. There appeared to be abundant nectar production during these periods.

Time per foray was noted for 45 bees, the shortest time in an area being 13 seconds, and the longest time 5432 seconds with an average of 558 seconds. Time actually in the flower was noted for 72 *Bombus* visits, the shortest being three seconds and the longest 270 seconds for an average of 53 seconds per visit.

On different days of another season (1981), 82 flower visits were tabulated for flower entrance/exit mode. There was no breakdown for size or species since I was interested in total effective pollinator activity. Stigma, intermediate and petal entrances or exits have been defined above. Sixty-three (76.8%) flower entrances were over the stigma, 18 (21.9%) were intermediate, and only one (1.2%) entrance was beneath a petal. In the exit phase, 45 (54.9%) of the exits were intermediate, 28 (34.1%) were over the stigma, and 9 exits (11.0%) were from beneath a petal with no stigma contact.

DISCUSSION

Results of my flower bagging experiments concur with those of Burr (1979) who did a thorough pollination study of another *Sarracenia* sp., *S. purpurea* ssp. *purpurea*, in Vermont bogs. She also had no seedset. However, Mandossian (1965), who made some pollination comments in a thesis concentrating on the ecology of *S. purpurea* in Michigan bogs, did get some seedset in bagged flowers, although with just a very few seeds in a few flowers. Considering Burr's results and my own, and my experience with growing some Sarracenias in insect-proof greenhouses over the years, I suspect that Mandossian's bagging may have been somewhat "leaky".

Nectar "sugar" content range is held to be 25-75% in flowers generally (Faegri & van der Pijl, 1979), and the 39% result in *S. flava* is within this range. As stated previously, there does not seem to be much data on total flower pollen weights, but *S. flava* clearly produces large quantities that often gather to some depth in the umbrella cup if protected from insects.

Since bagged (and greenhouse protected flowers) do not set seed, and an external pollinator is likely (as also suggested by some earlier field botanists by presumption and deduction from flower structure; e.g. James, 1883; Higley, 1909), some facets of the pollinator's activity may be predicted. The pollinator would have to pass by "choice" or compulsion directly over the stigma knob villous tip to effect pollination; a far lateral brush of the column would likely not do it, this deduced from the villous receptor surface morphology as noted above. The pollinator would therefore have to be large and strong enough to be compelled to force its way over the stigma knob between petals, rather than being smaller and entering the flower by bypassing the stigma knob. My observations of *Bombus* spp. fit this situation well.

Burr (1979) also noted that *Bombus* was the primary pollinator in her Vemont bog *Sarracenia purpurea* plants, and she noted no *Apis mellifera* activity at all. In contrast, Jones (1908, 1935), after first ruling out night pollinators which he intially suspected empirically (also ruled out by me for *S. flava* as in Jones, and by Burr in *S. purpurea*), thought that *A. mellifera* was the primary pollinator of *S. flava* in Carolinian coastal plain savannas, but in his later paper felt that many insects were equally capable of pollinating the species including beetles, something I did not find. Again, mentioning a parallel in the sister species *S purpurea*, Mandossian (1965) also felt that *A. mellifera* was the primary pollinator in Michigan bogs, but conceded that *Bombus* spp. were also capable of accomplishing this, their activity being described as "spectacular". Since *S. purpurea* has a smaller and more closed flower with the petals often clasped over the outer surface of the umbraculum when in full anthesis in northern bogs, quite possibly honeybees and other smaller insects could achieve pollination, but Mandossian does not seem to have studied relative numbers of insects actually working the flowers and details of their activities, such as entrance and exit.

One must also recall that *Apis mellifera* is essentially an exotic introduction into North America (Faegri & van der Pijl, 1979), and

in a longterm evolutionary sense would likely not have significant effects thus far on relatively long-lived perennials, although there might be some short term effects on recent hybridization patterns in more open, disturbed bogs.

My observations on *Bombus* flower entrance and exit modes in *S. flava* are roughly similar to Jones (1908, 1935) in broad concepts although his descriptions lack detail and imply a rather constant petal exit mode. Burr (1979) described very similar detail in *Bombus* entrance into flowers of *S. purpurea*, but did not mention details of exit.

Jackson (1881) noted that on a cloudy day with a thunderstorm imminent, *flies* (italics mine, possibly *Sarcophaga sarraceniae*?) were noted in the flower cavity of *S. purpurea* where he thought they were "eating the pollen, of which scarcely a grain could be seen". Higley (1909) also thought that "dipterids" were the pollinators of *S purpurea* in Illinois since he saw many entering and leaving the flowers with liberal dustings of pollen on their backs. Jones (1908, 1935) also thought that the *Sarracenia* fly might at least play some role in pollination of *S. flava*. However, Burr (1979), aware of these assertions and looking specifically for some *Sarcophaga* pollination activity, failed to note any in *S. purpurea* in Vermont, mentioning that the flies seemed more to be seeking refuge in the flower in inclement weather (see Jackson reference above) and did not effect pollination. She further noted, as I did, that the flies are actually not sufficiently hirsute to carry a significant pollen load from flower to flower.

Several authors have claimed that the flowers of *Sarracenia* spp. are protandrous (Macfarlane, 1893, 1908; Jones, 1908, 1935; Uphof, 1935) while Burr (1979) demonstrated that pollen readily germinated on the stigma knob surface of *S. purpurea* in Vermont the first day of anthesis (and even before in loose buds) using special staining and surface microscopic techniques. Older claims for protandry have never been supported by references or evidence and one feels that the concept "just grew" or was repeated by assumption through the years. My studies, using a different approach than Burr, indicate that in *S. flava* the flowers are not protandrous.

It is interesting to postulate whether olfactory or visual stimulus serves as the primary attractant of pollinators in *Sarracenia flava*. Faegri and van der Pijl (1979) suggest that as a general rule, a straight approach to a flower by a pollinator indicates visual

stimulus, while an irregular approach indicates olfactory stimulus, particularly if from downwind. Using this concept, the *Bombus* approach to *S. flava* that I noted seems to be one of visual for distance and olfactory for close-in confirmation. Valentine (1975) concluded that the flower color yellow is adaptively neutral and that unspecialized anthophiles were yellow, thus indicating some color attraction value, although vaguely so. However, Woodell (1978) concluded that *Bombus* tends to fly upwind to land on flowers for aerodynamic reasons and that the circling, zig-zag approach is for the purpose of seeking correct orientation to wind direction. In fact, I noticed the irregular initial close-in approach on perfectly calm days as well. I would further point out my observations that the bees would sometimes approach green, closed flower buds but from which *S. flava* flower fragrance could be detected. The latter could make a case for at least some olfactory stimulation, but Faegri and van der Pijl (1979) suggest that bees may learn to recognize the form of the whole plant as well and thus approach unopened buds for that reason.

Since I also have noticed *Bombus* approaching and landing on green, tightly closed but odoriferous buds in bogs in which *no* flowers had yet opened and in which there were no spring pitchers yet, and considering the life history of the genus (Heinrich, 1979) and the naiveté of early spring queens, this would hardly seem to be a learned activity of recognized plant form. Burr (1979) concluded in *Sarracenia purpurea* that visual and olfactory stimuli were both important, and in general Heinrich (1979) and Faegri and van der Pijl (1979) conclude that visual perception is used by *Bombus* spp. for distance orientation, and olfactory perceptions for close-in confirmation. I would, on balance, favor this combined concept in the case of *S. flava*.

There are several possibilities in the pollination results based on observing the entrance and exit modes of *Bombus* in *Sarracenia flava* flowers. Entrance would result in bringing to the stigma knob pollen from a previous flower visit, which might be the same flower since bees were occasionally observed to revisit the same flower immediately or some time later in the foray in which case selfing would occur. Or, pollen from another flower could result in either geitonogamy or xenogamy. If exit were over the stigma knob, or an effective intermediate exit, selfing would again be likely. Even

though a bee exited over a stigma knob and most certainly deposited some isogenous pollen on the stigma, one must realize that this pollen is likely mixed in the bee's pile with pollen from other flowers and that partial or mixed cross-pollination would still be possible to some extent. Further, the bee might mix exogenous pollen into the "pool" already present in the umbraculate cup.

Also, since flowers were open from five to ten days, it seems likely that pollen deposited on early days had already germinated and pollen tubes were growing and that later pollinations would be inconsequential. Sarracenias produce large quantities of pollen compared to the total small stigmatic receptor surface of a flower and there may be some competition among growing pollen tubes or even those grains germinating on the villous surfaces (as with other genera in Ter-Avanesian, 1978). The comparatively huge *Bombus* pile surface again compared to the small stigma knob surface would tend to rather massive applications of pollen. Ter-Avanesian has postulated that the quantity of pollen applied to a flower stigma may influence variation patterns and evolutionary trends. Fewer grains reduce pollen tube competition and in his observations of other plant species result in more variation, while massive pollinations result in more tube competition and more uniform progeny.

Bombus syndrome flowers tend to be large with abundant hidden nectar (Faegri & van der Pijl, 1979; Heinrich, 1979) and *Sarracenia flava* flowers are certainly so. In addition, as noted above, they have a large ratio of pollen production to total stigma receptive surface. The pollen is also well concealed and protected from wind and rain (as noted by Higley in *S. purpurea*, 1909) and few casual visitors enter the flower. The abundant nectar production allows a bee to remain with a flower for a longer period of time than in smaller flowers or those otherwise producing less nectar. Heinrich (1979) has brilliantly summarized energy economics of bumblebees and indicated that the energy demands of the insects, especially early spring queens, do not permit wasted activity but that the bee is on a slim margin of reserve under the best foray circumstances. In any foray, the bee will necessarily visit more flowers that have less nectar and therefore expend more energy than in flowers with greater nectar quantities. Valuable energy is consumed flying among low nectar producers while large nectar producers allow a somewhat more leisurely approach in relative terms. This all seems to be reflected in the

time per flower observations I made above, and which Burr (1979) similarly noted in *S. purpurea*. The greater collection time per unit in a foray energy expenditure also indicates some degree of constancy and that the bees learned the flowers well (Grant, 1963). In fact, during the early days of anthesis in a bog, many of the bees (especially larger species) appeared quite clumsy in their entrance exit activities. Later in anthesis, little difficulty was evident.

Re-entry into the same flower in sequence or later in a foray was also noted by Heinrich (1979) in other flower species, and he felt this might be related to the relative energy profitability of the flower or plant species as a whole. *Bombus* tends not to range far from good, learned nectar sources.

Macfarlane stated that mixing of nectar and pollen in the umbraculum cup was necessary for good pollen tube germination (1893, 1908) although he never documented this. I have seen nectar drops collect in the umbrella cup only in plants grown in the greenhouse or otherwise protected from insects. Furthermore, there is some question about the viability of pre-moistened pollen (Faegri, 1978; Faegri & van der Pijl, 1979).

Last to be considered is Jones' theory about the importance of the post-anthesis flower resuming an erect position (1908, 1935). Early in the growing season, the solitary bud is atop an erect scape as is the case with most flowers. As anthesis approaches, the top of the scape bends into a shepherd's crook shape so that the flower is pendulous. As anthesis ends and the petals begin to wither, the flower often—but not always—begins to resume a more erect character to varying degree. Jones felt that this was an important event in that it allowed residual pollen in the umbrella cup to fall over stigmas in case they had not been pollinated. He also felt that there was still continued pollinator activity even after petal-fall.

I do not consider this concept viable for the following reasons. In the first place, by the time the petals and stamens are shed or are in the process of doing so as the flower resumes a more erect position, the umbraculum is empty of pollen in the field, and the intense *Bombus* activity of days before has more than likely resulted in pollination with pollen tube growth well along. Also, nectar secretion ceases and the fragrance is remarkably reduced (due probably to loss of petals wherein most odor production resides, v.s.), and of course the bright yellow petals with their visual attractive value are

gone. Jones also assumes a long protandrous period of possibly three days to two weeks which has been contradicted in my study, and with *S. purpurea* (Burr, 1979). Finally, the geometry of the flower is not right for any pollen that might have been left in the umbrella cup to fall over a stigma knob when the flower is tilted back into an erect position. I stripped fresh flowers of petals and filled the cups with some red dye powder while the flower was in a pendulous position. Then by hand, I slowly turned the flower up on the scape axis to an erect position. None of the dye powder actually fell on villous stigma surfaces. The resumption of an erect position by some *Sarracenia* flowers late in anthesis is an interesting phenomenon that still awaits elucidation.

SUMMARY

In a field study, the primary pollinator of *S. flava* was found to be *Bombus* spp. At best, *Apis mellifera* and small native bees might be accidental pollinators. *Sarcophaga sarraceniae* was found not to be a pollinator. The flowers of the species are not protandrous, and a previous theory on the importance of flower erection late in anthesis for late self pollination has been contradicted. Considering pollinator activity, results can be selfing, geitonogamy, or xenogamy.

LITERATURE CITED

Burr, C.A. 1979. The pollination ecology of *Sarracenia purpurea* in Cranberry bog, Webridge, Vermont (Addison Co.). Masters thesis, Middlebury College, Middlebury, VT.

Faegri, K 1978. Trends in research in pollination ecology. *In:* A.J. Richards (Ed.), The pollination of flowers by insects, p. 5-12. Academic Press, New York. 213 p.

Faegri, K., & L. van der Pijl. 1979. The principles of pollination ecology. Pergamon Press, New York., 244 p.

Grant, V. 1963. Origin of adaptations. Columbia University Press, New York. 606 p.

Heinrich, B. 1979. Bumblebee economics. Harvard University Press, Cambridge, MA. 245 p.

Higley, W.K. 1909. The northern pitcher plant or the side-saddle flower, *Sarracenia purpuea* L. Bull. Chic. Acad. Sci. **1**: 41-55.

Jackson, J. 1881. *Sarracenia purpurea* L. Bot. Gaz. **6**: 242.

James, J.F. 1883. Pitcher plants. Am Natural. **17**: 283-293.

Jones, F.M. 1908. Pitcher-plant insects—III. Entom. News **19**: 150-156.

———. 1935. Pitcherplants and their insect associates. *In*: Mary Vaux Walcott, Illustrations of the North American pitcherplants. Smithsonian Institution, Washington, D.C. 27 p.

KEVAN, P.G. 1978. Floral coloration, its colorimetric analysis and significance in anthecology. *In*: A.J. Richards (Ed.), The pollination of flowers by insects. p. 51-78., Academic Press, New York. 213 p.

_____. 1979. Vegetation and floral colors revealed by ultraviolet light: Interpretational difficulties for functional significance. Amer. J. Bot. **66**: 749-751.

MACFARLANE, J.M. 1893. Observations on pitchered insectivorous plants (Part II). Ann. Bot. 7: 403-458.

_____. 1908. Sarraceniaceae. *In*: A. Engler, Das Pflanzenreich, IV. 110., p. 1-39.

MANDOSSIAN, A.J. 1965. Some aspects of the ecological life history of *Sarracenia purpurea*. Michigan State University Ph.D. dissertation, East Lansing (University Microfilms, Ann Arbor, MI 48106, No. 65-14245). 161 p.

MCDANIELS, S. 1971. The genus *Sarracenia* (Sarraceniaceae). Bull. Tall Timbers Research Station (Tallahassee, FL), No. **9**. 36 p.

MITCHELL, T.B. 1960, 1962. Bees of the eastern United States. North Carolina Agricultural Experimental Station, Raleigh. Tech. Bull, No. **141** (vol. 1, 1960) and No. **152** (vol. 2, 1962), 538 and 557 p.

RUSSELL, A.M. 1918. The macroscopic and microscopic structure of some hybrid Sarracenias compared with their parents. Bot. Contrib. Univ. Penn. **5**: 3-41.

SCHNELL, D.E. 1976. Carnivorous plants of the United States and Canada. John F. Blair, Publisher, Winston-Salem, N.C. 125 p.

_____. 1978a. *Sarracenia flava* L. Infraspecific variations in eastern North Carolina. Castanea **43**: 1-20.

_____. 1978b. Systematic flower studies of *Sarracenia* L. Castanea **43**: 211-220.

TER-AVANESIAN, D.V. 1978. Significance of pollen amount for fertilization. Bull. Torrey Bot. Club **105**: 2-8.

UPHOFF, J.C.T. 1936. Sarraceniaceae. *In*: A. Engler & H. Harms, Die naturlichen pflanzenfamilien, 2nd ed. Bd. 17b, p. 1-24.

VALENTINE, D.H. 1975. The taxonomic treatment of polymorphic variation. Watsonia **10**: 385-390.

WOODELL, S.R.J. 1978. Directionality in bumblebees in relation to environmental factors. *In*: A.J. Richards (Ed.), The pollination of flowers by insects. p. 31-39. Academic Press, New York. 213 p.

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DISTRIBUTIONAL STUDIES OF MASSACHUSETTS BRYOPHYTES

BRENT D. MISHLER AND NORTON G. MILLER

ABSTRACT

Eighteen bryophytes new to Massachusetts and fifty-five additional new county records are reported, including the second collection of *Pseudocrossidium hornschuchianum* from the New World. Significant range extensions are briefly discussed in an annotated list, and additional noteworthy records are presented in an appendix. The bryophyte flora of the state as documented in the literature now stands at 329 species of mosses and 144 species of liverworts.

Key words: bryophytes, mosses, liverworts, floristics, phytogeography, autecology

Recent fieldwork in several parts of Massachusetts has led to the discovery of range extensions for a number of species of mosses and liverworts. These noteworthy collections are presented here to update the published catalogs of the moss and hepatic floras of Massachusetts (Hilferty, 1960; Evans, 1923). The ecological and biogeographic significance of the new distributional information is also discussed briefly.

Eighteen bryophytes new to the state, and twenty-three significant range extensions within the state are given in an annotated list. Thirty-two additional new county records are provided in an appendix. New records of *Sphagnum* are not given in this paper because these will be reported at a later time by Miller and Andrus.

Early publications treating the Massachusetts bryoflora are cited by Evans (1923) and Hilferty (1960). Judd (1980) studied bryophytes of the peat mat at Ponkapoag Pond, Canton, Norfolk County, and reported one new state record: *Plagiothecium laetum*. Schuster (1981) discussed probable late Pleistocene relict liverworts that grow in extremely limited microhabitats in the Green River valley, Colrain, Franklin County. He reported seven new state records: *Jungermannia cordifolia, Scapania gymnostomophila, Lophozia gillmanii, L. bantriensis, L. heterocolpos, L. badensis,* and *Pellia megaspora*.

The prevailing acidic soils and bedrock over much of the state result in a rather uniform bryoflora, especially east of the Connecticut Valley. However, Schuster's studies, as well as our own, indicate that despite no lack of general collecting of bryophytes in Massa-

chusetts, there remains a great need for careful collecting at ecologically special sites. The studies summarized here are certainly not exhaustive; further work at these and similar places will be productive.

A few small and scattered exposures of marble occur among the predominant granites, gneisses, and schists of eastern Massachusetts. Cook (1974) presented detailed geological studies of the pre-Devonian Nashoba Formation, a northeast-southwest trending belt of lenses of siliceous marble and dolomite. Using topographic maps presented by Cook, we located several occurrences of rocks of this formation. Most were roadcuts or old quarries, some of which proved to be quite disturbed and barren of all but weedy species of bryophytes. However, the following occurrences of the Nashoba Formation (discussed below) produced significant collections of calcicolous bryophytes: Bolton, Boxborough, and Estabrook Woods.

The Third A. LeRoy Andrews Bryological Foray, organized and led by N. G. Miller in 1978, visited two interesting and imperfectly collected sites in central Massachusetts: Roaring Mountain, a site with a steep, extensive outcrop of conglomerate (calcareous in places); and Tom Swamp, a large bog and associated black spruce-tamarack forest. During pre-foray exploration, the foray itself, and later studies of the vegetation of Tom Swamp by Miller and R. H. W. Bradshaw, several state and numerous county records were noted, as discussed below.

Western Massachusetts provides the only extensive marble deposits in the state, and these occur in north-south trending bands in valleys between the Taconic Range and the Berkshire Mountains. Bartholomew's Cobble along the Housatonic River in the southwestern corner of the state has long been famous for its highly diverse flora (Arnold & Bailey, 1965). Six hundred and eighty-eight taxa of tracheophytes, including fifty-one ferns and fern allies, occur on the approximately 250 acres of the Bartholomew's Cobble Reservation (Boutard & VanWart, 1981). The habitat diversity responsible for this remarkable flora is provided in part by a mixture of dolomitic marble and quartzite that forms steep, rocky knolls with many ledges and boulders (Arnold & Bailey, 1965). Because the bryophyte flora was little-known, collections were made by one of us (BDM) as a contribution towards a revised list of the flora (to be published by

the Massachusetts Trustees of Reservations). In a two-day period 118 species of bryophytes (including 12 new to the state) were collected.

The following is an alphabetical list of localities at which collections were made.

Bartholomew's Cobble—Berkshire County: Bartholomew's Cobble Reservation, Ashley Falls, 4 mi. S of Sheffield, along the Housatonic River, ca. 700 ft. elev.

Bolton Worcester County: abandoned limestone quarries, 2.4 mi. E of Bolton Center, off Route 117, ca. 300 ft. elev.

Boxborough—Middlesex County: abandoned limestone quarry, 0.7 mi. SW of Liberty Square in Boxborough, on E side of Hill Road, ca. 330 ft. elev.

Breakheart—Essex County: Breakheart Reservation, ca. 2 mi. NW of Saugus, NE corner of Reservation near small pond in Saugus River drainage, ca. 50 ft. elev.

Estabrook Woods Middlesex County: abandoned limestone quarries, Estabrook Woods, Concord Field Station of the Museum of Comparative Zoology, Harvard University, ca. 4 mi. N of Concord Center, on W side of Estabrook Road, ca. 240 ft. elev.

Roaring Mountain—Franklin County: E slope of Roaring Mountain, southern edge of Mt. Toby State Forest, ca. 7 mi. S of Millers Falls on Route 63, 450-800 ft. elev.

Sudbury River—Middlesex County: between Martha's Point and Lee's Cliff, W side of Sudbury River, ca. 3 mi. S of Concord Center, ca. 130 ft. elev.

Tom Swamp—Worcester County: Tom Swamp, between Riceville and Brooks Ponds, Harvard Forest, ca. 2 mi. NW of Petersham, ca. 760 ft. elev.

An annotated list of species with range extensions of ecological and distributional significance follows. In the interest of completeness, additional new county records are listed in an Appendix. The sequence and nomenclature are according to Stotler and Crandall-Stotler (1977) for liverworts and Crum, Steere, and Anderson (1973)

for mosses. Voucher specimens for all of the reported taxa are on deposit in the Farlow Herbarium of Harvard University. Our individual collections are cited with initials (BDM or NGM) and collection number. New state records for Massachusetts are marked with an asterisk.

HEPATICAE

ADELANTHACEAE

Odontoschisma sphagni Breakheart, *NGM 8206*; peaty soil, summit of a low ridge of soil extending out into a pond. The only other known collection from Massachusetts was reported by Schuster (1974) from Cape Cod, Barnstable Co. According to Schuster, this species is rare in North America with a strictly oceanic distribution from Newfoundland to Massachusetts.

JUBULACEAE

Frullania riparia Bartholomew's Cobble, *BDM 1684*; Roaring Mountain, *NGM 8248*; face of steep rock outcrops and boulders. Cited by Evans (1923) only as a literature record. Widespread in eastern North America.

METZGERIACEAE

***Metzgeria furcata** Bartholomew's Cobble, *BDM 1698, 1838*; on both basic and acidic rock. In North America, occurring on the West Coast and broadly in the East.

MUSCI

ANDREAEACEAE

Andreaea rupestris Sudbury River, *NGM 8903*; dry face of bluff. Previously reported in Massachusetts from the Mt. Greylock region, Berkshire Co., and from Norfolk Co. Based on specimens annotated by W. Schultze-Motel in the Farlow Herbarium, the plants from Norfolk Co. can all be referred to *A. rothii*. In North America, *A. rupestris*

occurs across boreal and north temperate regions, particularly in mountainous areas of the East and West.

FISSIDENTACEAE

***Fissidens obtusifolius** — Bartholomew's Cobble, *BDM 1690*; marble boulder near stream (confirmed by R. A. Pursell). According to Crum and Anderson (1981), endemic to eastern North America, from Ontario and Massachusetts south.

Fissidens subbasilaris—Estabrook Woods, *NGM 8677*; Roaring Mountain, *NGM 8430*; soil, crevices and base of steep rock faces. Previously reported in Massachusetts only from Bristol Co.; widespread in eastern North America from New England and Ontario south (Crum & Anderson, 1981) and most often growing on tree trunks.

DICRANACEAE

***Dichodontium pellucidum** Roaring Mountain, *Zander 4700*; dried up stream bed. Listed as doubtful for Massachusetts by Hilferty; a calcicole, widespread in northern and montane regions of North America.

ENCALYPTACEAE

Encalypta procera Bartholomew's Cobble, *BDM 1711*; Estabrook Woods, *NGM 8672*; Roaring Mountain, *NGM 8428*; calcareous soil and rock. Previously reported in Massachusetts from Hampshire and Worcester Cos. Widespread across northern and eastern North America; expected in other regions of calcareous rock in the state.

POTTIACEAE

Gymnostomum aeruginosum—Roaring Mountain, *NGM 8241*; damp conglomerate boulder. An obligate calcicole, previously known in Massachusetts only from Berkshire Co.; widespread in North America.

Trichostomum tenuirostre– Estabrook Woods, *NGM 8670*; Roaring Mountain, *NGM 8226*; damp, vertical marble and conglomerate rock. Previously known in Massachusetts only from Berkshire Co.; widespread in North America.

***Hyophila involuta**—Bartholomew's Cobble, *BDM 1788*; wet marble boulder near stream; a calcicole, sporadically distributed throughout eastern North America.

Didymodon rigidulus—Estabrook Woods, *NGM 8671*; damp, vertical limestone. Previously known in Massachusetts only from Berkshire Co.; a calcicole, widely distributed in eastern North America.

Bryoerythrophyllum recurvirostrum Bartholomew's Cobble, *BDM 1858*; Roaring Mountain, *NGM 8421*; Sudbury River, *NGM 8907*; rock and soil, usually calcareous and near water. Previously known in Massachusetts from Plymouth Co.; widespread in North America.

Barbula convoluta– Bartholomew's Cobble, *BDM 1859*; Bolton, *BDM 3679*; sunny, disturbed, calcareous soil. A calcicole, previously known in Massachusetts only from Bristol Co.; widespread in North America.

***Pseudocrossidium hornschuchianum**—Bartholomew's Cobble, *BDM 1705*; dry, sunny limestone outcrop (det. R. H. Zander). This is the second collection of *P. hornschuchianum* known to us from the New World; the only other station is a botanical garden in Vancouver, British Columbia (Tan, Zander & Taylor, 1981). The species is common in Europe at disturbed sites along roadsides and on stone walls (ibid.). The species may have been introduced from Europe, or it might occur unrecognized elsewhere in North America.

***Tortula mucronifolia** Bartholomew's Cobble, *BDM 1826, 3721*; sunny calcareous sand over limestone, bank of river. Reported as doubtful for Massachusetts by Hilferty; occurs otherwise at scattered calcareous sites in New York and western Vermont; common further north, from Labrador and Greenland to Alaska, and south through the western United States.

Tortula ruralis—Bartholomew's Cobble, *BDM 1704*; thin soil over marble, in dry, sunny locations. The only other reported locality for this species in Massachusetts is Nahant, Essex Co., where there is a small outcrop of calcareous Cambrian limestone at East Point (G. Thompson, pers. comm.). A search of this locality in 1979 showed it to be devoid of *T. ruralis*. This moss is a calcicole, common in western North America and across Canada, especially in the Arctic; it occurs sporadically in the Great Lakes region, New York, and western Vermont.

Grimmia pilifera—Bartholomew's Cobble, *BDM 1741*; quartzite boulder. Reported by Hilferty only from eastern Massachusetts; throughout eastern North America.

BRYACEAE

Pohlia wahlenbergii—Bartholomew's Cobble, *BDM 1857*; Roaring Mountain, *NGM 8240*; moist soil and rock, bank of river and conglomerate outcrop. Previously reported in Massachusetts only from Bristol Co.; widespread in North America.

MNIACEAE

***Mnium medium**—Bartholomew's Cobble. *BDM 1766*; moist soil, base of limestone cliff. Widespread in North America.

Mnium thomsonii (*M. orthorrhynchum*)—Estabrook Woods, *NGM 8674*; Roaring Mountain, *NGM 8436*; damp calcareous rock in quarry, and soil at base of conglomerate rock. Previously known in Massachusetts only from Berkshire Co.; widespread in North America. According to Crum and Anderson (1981): "frequently but not always in calcareous habitats."

BARTRAMIACEAE

***Plagiopus oederiana**—Roaring Mountain, *NGM 8243*; rock, face of conglomerate outcrop. Listed as doubtful for Massachusetts by Hilferty. According to Crum and Anderson (1981), on cliffs and boulders (especially calcareous rock);

in North America occurring across the Arctic and south in montane or rocky areas to Oregon, Colorado, and Virginia.

ORTHOTRICHACEAE

***Zygodon viridissimus** var. **rupestris**—Bartholomew's Cobble, *BDM 1801*; sunny bark of old apple tree. In North America with a scattered but widespread distribution.

***Amphidium mougeotii**—Roaring Mountain, *Zander 4701*; rock ledges. Widespread on acidic rocks in mountainous regions of North America.

Orthotrichum anomalum—Bartholomew's Cobble, *BDM 1809*; Boxborough, *BDM 3680*; Estabrook Woods, *BDM 1621*; calcareous rock. Previously reported in Massachusetts from Bristol and Essex Cos. According to Vitt (1973), in North America across the North, in the East almost exclusively on calcareous rock north of the line of maximum glaciation, and in the West on both basic and acidic rock southward in the Rocky Mountains.

Orthotrichum pumilum—Bartholomew's Cobble, *BDM 1802*; sunny bark of old apple tree. Previously reported in Massachusetts from Bristol Co.; widespread in North America, mostly south of Canada.

FONTINALACEAE

***Fontinalis hypnoides**—Bartholomew's Cobble, *BDM 1765*; attached to rocks in slow moving brook. Widespread in northern and western North America.

LESKEACEAE

***Lindbergia brachyptera**—Bartholomew's Cobble, *BDM 1803*; sunny bark of old apple tree. Widespread in eastern North America.

Leskea gracilescens—Bartholomew's Cobble, *BDM 1800*; Roaring Mountain, *Allen 795*; bark of deciduous trees and on quartzite and conglomerate rock. Previously reported from Middlesex Co.; endemic to the deciduous forests of eastern North America.

THUIDIACEAE

Haplohymenium triste—Bartholomew's Cobble, *BDM 1693*; marble and quartzite ledges and cliffs. Previously reported only from Bristol Co.; widespread in eastern North America, but according to Crum and Anderson (1981), usually on trees and rarely on rock.

Anomodon minor—Bartholomew's Cobble, *BDM 1794*: shaded marble cliffs. Widespread in eastern North America, most often on trees but sometimes on calcareous rocks (Crum & Anderson, 1981).

***A. viticulosus**—Bartholomew's Cobble, *BDM 1670*; Roaring Mountain, *NGM 8415*; marble and conglomerate rock, in crevices of cliffs. Listed as doubtful for Massachusetts by Hilferty; a calcicole distributed throughout eastern North America.

***Thuidium pygmaeum**—Roaring Mountain, *NGM 8442*; damp face of rock bluff. Previously known from southern Ontario and New York south to Florida and Arkansas (Crum & Anderson, 1981).

AMBLYSTEGIACEAE

***Calliergon stramineum**—Tom Swamp, *NGM 8830*; shallow depression in peat. Listed as doubtful for Massachusetts by Hilferty. Widespread across Canada and the northern United States, this apparently represents the southernmost locality for the species in New England.

BRACHYTHECIACEAE

Brachythecium digastrum—Bartholomew's Cobble, *BDM 1699*; both tree stumps and marble. Previously reported from Bristol and Worcester Cos.; endemic to eastern North America.

Bryhnia graminicolor—Roaring Mountain, *NGM 8447*; ledge of conglomerate bluff. Previously reported in Massachusetts only from Berkshire Co. Endemic to eastern North America, often on calcareous soil or rock (Crum & Anderson, 1981).

SEMATOPHYLLACEAE

***Brotherella tenuirostris**—Bartholomew's Cobble, *BDM 1841*; quartzite boulder. Endemic to eastern North America.

HYPNACEAE

Platygyrium repens Bartholomew's Cobble, *BDM 1712, 1757*; fallen logs and on rock. Common in central and eastern Massachusetts; widespread in northern and eastern North America.

Hypnum lindbergii Bartholomew's Cobble, *BDM 1830*; moist soil near river or springs. Previously reported from Massachusetts only in the east; widespread in North America.

Isopterygiopsis muelleriana Tom Swamp, *NGM 8821*; base of tree in wooded bog. In North America occurring in western and eastern Canada and in mountainous habitats in the eastern United States (Crum & Anderson, 1981).

Taxiphyllum deplanatum *Bartholomew's Cobble, BDM 1814*; Roaring Mountain, *NGM 8435*; moist soil near river or springs, and rock in talus below bluff. Endemic to North America, restricted to the east except for localities in Arizona and New Mexico (Ireland, 1969). According to Crum and Anderson (1981), the habitat is usually rock, nearly always calcareous in the northern part of the range.

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LITERATURE CITED

ARNOLD, H. J., & S. W. BAILEY. 1965. Bartholomew's Cobble, Sheffield, Massachusetts: Its geology, fauna and flora. Massachusetts Trustees of Reservations, Milton, Massachusetts.

BOUTARD, A., & G. F. VANWART. 1981. Checklist of vascular plants of Bartholomew's Cobble, Ashley Falls, Massachusetts. Massachusetts Trustees of Reservations, Milton, Massachusetts.

COOK, L.P. 1974. Metamorphosed carbonate rocks of the Nashoba Formation, eastern Massachusetts. Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts.

Crum, H. A., & L. E. Anderson. 1981. Mosses of eastern North America. 2 volumes. Columbia University Press, New York.

———., W. C. Steere, & L. E. Anderson. 1973. A new list of mosses of North America north of Mexico. Bryologist **76**: 85–130.

Evans, A. W. 1923. Second revised list of New England Hepaticae. Rhodora **25**: 192–199.

Hilferty, F. J. 1960. The mosses of Massachusetts: a county catalogue with annotations. Rhodora **62**: 145–173.

Ireland, R. R., Jr. 1969. A taxonomic revision of the genus *Plagiothecium* for North America, north of Mexico. Natl. Mus. Canada Publ. Bot. **1**: 1–118.

Judd, W. S. 1980. Bryophytes of the peat mat at Ponkapoag Pond, eastern Massachusetts, with taxonomic and ecological notes on *Sphagnum*. Rhodora **82**: 563–578.

Schuster, R. M. 1974. The Hepaticae and Anthocerotae of North America east of the Hundredth Meridian. Volume III. Columbia University Press, New York.

———. 1981. Late Pleistocene bryological relicts in western Massachusetts. Rhodora **83**: 441–448.

Stotler, R., & B Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. Bryologist **80**: 405–428.

Tan, B. C., R. H. Zander, & T. Taylor. 1981. *Pseudocrossidium hornschuchianum* and *P. revolutum* var. *obtusulum* in the New World. Lindbergia **7**: 39–42.

Vitt, D. H. 1973. A revision of the genus *Orthotrichum* in North America, north of Mexico. Bryophytorum Bibliot. **1**: 1–208 + 60 plates.

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Appendix. Additional Massachusetts County Records

Voucher specimens deposited in FH.

1. Franklin County (Roaring Mountain):

Brachythecium oxycladon—*NGM 8227*

B. salebrosum—*NGM 8420*

Bryum pseudotriquetrum—*NGM 8422*
Campylium chrysophyllum—*NGM 8423*
Climacium americanum—*BDM 1257*
Dicranum fulvum—*NGM 8228*
D. montanum—*BDM 1262*
Diphyscium foliosum—*BDM 1242*
Eurhynchium pulchellum—*BDM 1283*
Fissidens cristatus—*NGM 8429*
Grimmia alpicola var. *rivularis*—*BDM 1260*
Homomallium adnatum—*NGM 8224*
Isopterygium elegans—*NGM 8234*
Leucobryum glaucum—*BDM 1274*
Mnium affine—*BDM 1247*
M. marginatum—*NGM 8232*
M. stellare—*NGM 8230*
Paraleucobryum longifolium—*BDM 1279*
Platygyrium repens—*NGM 8229*
Timmia megapolitana—*NGM 8444*
Tortella humilis—*NGM 8446*
Ulota hutchinsiae—*BDM 1264*

2. Worcester County (Tom Swamp):
Anacamptodon splachnoides—*NGM 8777*
Cephalozia pleniceps [not listed by Evans, 1923; but reported from Worcester County by Schuster, 1974]—*NGM 8717*
Herzogiella turfacea—*NGM 8714*
Hypnum fertile—*BDM 1293*

3. Worcester County (Bolton):
Barbula unguiculata—*BDM 3669*
Bryum lisae var. *cuspidatum*—*BDM 3675*
Mnium marginatum—*NGM 8916*
M. stellare—*NGM 8935*
Tortella humilis—*NGM 8929*
Weissia controversa—*BDM 3674*

SCLEROLEPIS UNIFLORA (COMPOSITAE) IN NEW ENGLAND

LESLIE J. MEHRHOFF

According to floristic manuals, *Sclerolepis uniflora* (Walt.) BSP is found in shallow water in coastal states from Alabama and Florida to New Jersey, with anywhere from 2 to 4 disjunct populations in New England (Fernald, 1950; Gleason & Cronquist, 1963; Seymour, 1969). Its distribution in New England is pertinent for phytogeographic reasons, as well as current rare plant concerns. Historic documentation of this species in New England and the actual number of stations in New Hampshire, Massachusetts and Rhode Island are clarified below.

NEW HAMPSHIRE POPULATION

The first report of *Sclerolepis uniflora*, then called *Sclerolepis verticillata* Cass., from New Hampshire was made by Dr. Frederic T. Lewis, a physician from Cambridge, Massachusetts in the October 1905 issue of RHODORA (Lewis, 1905). Lewis wrote that "...the occurrence of this species in Bradford, New Hampshire, a town some thirty-five miles north of Massachusetts and sixty miles from the coast, is of certain interest." In the same article he gives a specific locality in that town, "At the south end of Bradford Pond..." Bradford Pond later came to be known as Lake Massasecum. He states that he collected specimens "During the first week of August (1905)...". Lewis closes his note by saying, "Specimens collected at Bradford have been deposited in the Gray Herbarium of Harvard University." Fernald (1950) cites Lake Massasecum, Bradford, New Hampshire, as the only locality in that state. Seymour, in his *Flora of New England* (1969) cites two localities in New Hampshire, Bradford and Warner. Seymour frequently cited herbaria where he found exceptional records, and if no herbarium was cited it was understood that the record was from the New England Botanical Club Herbarium. There is a specimen of *Sclerolepis uniflora* in that herbarium collected by F. T. Lewis from a "sandy bog," Warner, New Hampshire, in August 1905. There are no other Lewis collections of *Sclerolepis uniflora* nor any other collection of that species from that year. A single Lewis collection of

S. uniflora with exactly the same data is on deposit in the Gray Herbarium.

In October 1928, Henry K. Svenson and Merritt L. Fernald visited Lake Massasecum (Bradford Pond) while on a collection trip in the region. Svenson (1929) mentions *Sclerolepis* as still existing at the south end of Lake Massasecum, where Lewis had found it in 1905, but made no mention of a station in Warner, a few miles away.

I suspect that the confusion regarding a locality for *Sclerolepis* in Warner has arisen because Lewis could have come to Lake Massasecum directly from Warner without going near the village of Bradford, as one would do today. He may have come from Warner on roads that cross a low mountain range locally known as the Mink Hills. These roads were actively used in the early 1900's, although they are now largely impassable. The southern end of the lake lies along one of these roads, only 0.4 miles from the Warner town line. Lewis may not have realized that he was at Lake Massasecum when he collected the specimens, or that he was in Bradford instead of Warner. By the time that his note appeared in RHODORA 2 months later, he apparently clarified his exact locality and reported it in RHODODRA as Bradford. Further support is given to this hypothesis by Svenson's 1929 article because he refers only to Lake Massasecum as the New Hampshire locality for *S. uniflora*. It is conceivable that Fernald had met Lewis and had been told the correct locality, rather than learning it only from the specimen labels. In his article on *Sclerolepis uniflora* in Massachusetts, Fernald (1912) mentions Dr. Lewis's station at Bradford, not Warner, as label information would have indicated.

Other reports continue to mention Bradford as the New Hampshire locality for *Sclerolepis*. The "Preliminary lists of New England plants XXIX" (Knowlton, *et al.*, 1925) states, "*Sclerolepis uniflora* is known from a pond in Bradford, New Hampshire . . .," obviously discounting the Warner locality.

In 1978, while living on Lake Massasecum, I decided to look for *Sclerolepis*. On 24 Sept. 1978, J. J. Dowhan and I visited the southeast end of the lake and there found many of the associated species mentioned by both Lewis and Svenson, as well as a large stand of *S. uniflora* (over 100 individuals) which appeared to be doing well. Being advised of its appearance we soon found many more indi-

viduals in other localites around the lake. Most individuals were vegetative, and nowhere was it as abundant as at the southeast end of the lake. A small swamp exists near the southeast end of the lake and this might have been Lewis's "sandy bog."

On 3 Aug. 1981 I visited the site on Lake Massasecum and found the plants almost in flower; on 29 Aug. 1981 I found numerous individuals in flower. I noted that the population appeared to have increased in number and size and seemed to be doing very well. Vegetative, submerged specimens also were found free-floating or rooted in the lake. Since this is an amphibious, heterophyllous species, the submerged, vegetative plants are easily overlooked. It was interesting to note that where the beach was manicured for a private swimming area no plants of *Sclerolepis* existed. A sharp demarcation between the two areas could be observed.

Between 1978 and 1981 I have searched other ponds in Warner and Bradford for *S. uniflora* wihtout success. Recently, another search of potential ponds in neighboring towns yielded nothing (D. Dunlop, pers. comm.). Considering the proximity of Lake Massasecum to the Warner town line, and the fact that in Lewis's day you could travel from Warner to Lake Massasecum without going through the village of Bradford, it is probable that the Warner locality on the Lewis specimens in the Gray Herbarium and the New England Botanical Club Herbarium is incorrect. All evidence points to only one locality for *Sclerolepis uniflora* in the state, Lake Massasecum, Bradford.

RHODE ISLAND-MASSACHUSETTS POPULATION

Sclerolepis uniflora was first discovered at Wallum Lake (then called Wallum Pond) in 1909 by J. Franklin Collins, H. W. Preston, and T. Hope (Collins, 1910). Wallum Lake straddles the Massachusetts-Rhode Island state line, with its northern part in the town of Douglas (Worcester County), Massachusetts, and its southern portion in Burrillville (Providence County), Rhode Island. Collins mentions only that his station was "...along the shore of Wallum Pond, in the town of Burrillville, Rhode Island," with no indication as to the proximity to the state line. He does not mention whether his group looked for this species on the Massachusetts end of the lake.

Because of Collins's report of this species from Wallum Lake in 1909, Merritt L. Fernald and F. F. Forbes visited the north end of the lake in Douglas, Massachusettts on 29 Oct. 1911, two years to the day after Collins had found *Sclerolepis* at the lake. They soon found the desired species within "a stone's throw of the northern end of the pond." They also found a station along the northeastern shore and "at every spring and seepy bank among boulders" along the western shore in both Massachusetts and Rhode Island (Fernald, 1912).

Fernald suggested searching other similar ponds in the vicinity for *Sclerolepis uniflora*, but no additional records seem to exist for this species, either in the literature or in the herbaria of the New England Botanical Club and Harvard University. Seymour (1969) cites only Wallum Lake, Massachusetts and Wallum Lake, Rhode Island as locations for this species in southern New England.

Stuckey (1977), in her report on the rare plants of Rhode Island says that it was found once at Wallum Lake and not seen since. Neither the report on the rare and endangered vascular plant species in Massachusetts (Coddington & Field, 1978) nor the report on the rare and endangered vascular plant species in Rhode Island (Church & Champlin, 1978) make reference to recent observations of this species at Wallum Lake or elsewhere in their respective states.

Accordingly, I visited Wallum Lake on 5 Sept. 1981 with O. Oliynyk to look for *Sclerolepis*. We followed the shoreline by canoe for much of its distance, beginning and terminating on the east side in Burrillville, Rhode Island. Although this method of search has its advantages, it does not allow for adequate coverage of every nook and cranny along the shoreline. Vegetative plants of *S. uniflora* were found between large boulders at the northern end of the Lake in Douglas, Massachusetts. There was no evidence of flowers or even buds on these plants, although from past experience with the New Hampshire population of this species, one should expect the plants to be flowering at this time of the year. Vegetative, submerged plants were also found floating in the water. Bruce Sorrie (pers. comm.) visited the lake on 24 Sept. 1981 and located *Sclerolepis* in both Massachusetts and Rhode Island along the western side of the lake, again without any signs of flowers or buds. On 13 Oct. 1983 I returned to Wallum Lake, this time in the company of Wm. Linke, to search for flowering individuals. This time we traveled by foot in

order to avoid missing any flowering material. Again, no flowering individuals were observed. The absence of flowering plants of *Sclerolepis* probably accounts for the lack of reports of this species at Wallum Lake in the past.

Copious amounts of dried algal material were observed along the shore as well as on many of the *Sclerolepis* plants. The abundance of algae was probably due to attempts at changing the pH of the lake by "liming" the lake during the winter, a practice employed by fishery programs as a management tool.

SUMMARY

For phytogeographic reasons it is prudent to consider that there are only two populations of *Sclerolepis uniflora* occuring in New England, one at Lake Massasecum, Bradford, New Hampshire, and the other at Wallum Lake, on the Massachusetts-Rhode Island state border. From a rare species habitat preservation point of view, we need to acknowledge that this species occurs in three New England states, Rhode Island, Massachusetts, and New Hampshire, and work to protect these habitats accordingly.

One fact is worthy of note for field botanists looking for this species in New England. I have observed abundant material of the aquatic, submerged form of this species occuring at both sites. This form only distantly resembles the emergent, erect plants with the stems of the aquatic form being longer and the leaves more loosely arranged. Fernald (1950) mentions parenthetically that the leaves are "in water flaccid and elongated." All too frequently we look for only the more easily observed flowering material; new stations for this species might be realized if floating aquatics in potential ponds are looked at closely. Investigations of drift lines at the windward ends of ponds or in coves where plant parts of such genera as *Myriophyllum*, *Vallisneria*, and *Potamogeton* can be found may prove fruitful.

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I would like to thank J. Dowhan, W. Linke, G. Mehrhoff, and O. Oliynyk for assistance in the field work; D. Dunlop and B. Sorrie for sharing their field observations with me; and G. Crow, G. Mehrhoff, and E. Pacala for their helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

CHURCH, G. L. & R. L. CHAMPLIN. 1978. Rare and endangered vascular plant species in Rhode Island. The New England Botanical Club in cooperation with the U.S. Fish & Wildlife Service. [Newton Corner, MA] 17 pp.

CODDINGTON, J., & K. G. FIELD. 1978. Rare and endangered vascular plant species in Massachusetts. The New England Botanical Club in cooperation with the U.S. Fish & Wildlife Service. [Newton Corner, MA] 51 pp.

COLLINS, J. F. 1910. *Sclerolepis uniflora* in Rhode Island. Rhodora **12**: 13.

FERNALD, M. L. 1912. *Sclerolepis uniflora* in Massachusetts. Rhodora **14**: 23-24.

_____ 1950. Gray's manual of botany, eighth edition. American Book Company. New York. 1361 pp.

GLEASON, H. A., & A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Co. New York.

KNOWLTON, C. J., C. A. WEATHERBY, & W. S. RIPLEY. 1925. Preliminary lists of New England plants - XXIX. Rhodora **27**: 57-64.

LEWIS, F. T. 1905. *Sclerolepis* in New Hampshire. Rhodora **7**: 186-187.

SEYMOUR, F. C. 1969. The flora of New England. Charles E. Tuttle, Inc. Rutland. 519 pp.

STUCKEY, I. H. 1977. Endangered plants of Rhode Island. Contribution No. 1794. University of Rhode Island Agricultural Experiment Station. Kingston, RI. 28 pp.

SVENSON, H. K. 1929. *Chamaecyparis thyoides* in New Hampshire. Rhodora **31**: 96-98.

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RELATIONSHIPS OF TWO ISOLATED GROUPS OF SUGAR MAPLES (*ACER SACCHARUM* MARSHALL SSP. *SACCHARUM*) IN WEST CENTRAL OKLAHOMA TO EASTERN AND WESTERN SPECIES

THOMAS C. DENT AND ROBERT P. ADAMS

ABSTRACT

Two groups of sugar maples in west central Oklahoma which have been described as relicts were compared by numerical methods to eastern and western U.S. references. The populations of the Wichita Mountains, Comanche Co. have previously been assigned to the equivalent of *Acer saccharum* Marshall subsp. *grandidentatum* (Torrey and Gray) Desmarais (sensu lato) by some authorities and to *Acer saccharum* Marshall subsp. *saccharum* by others. Those of the Caddo Canyons, Caddo and Canadian counties have been consistently designated as *Acer saccharum* Marshall subsp *saccharum*. The two groups have a north-south separation of ca. 80 km. The continuous range of *A. s.* subsp. *saccharum* penetrates eastern Oklahoma as an irregular fringe ca. 320 km east of the prairie groups. The closest stations for subsp. *A. s. grandidentatum* are ca. 480 km west of the Oklahoma locations in the Monzano Mountains of New Mexico and ca. 680 km southwest in the Edwards Plateau of Texas.

A principal coordinates analysis of micromeasurements of leaf samples from 160 populations collected in the four major geographic areas (eastern and western U.S. and Caddo Canyons and Wichita Mountains of Oklahoma) supports the hypothesis that the best designation for both Oklahoma groups is *A. s.* subsp. *saccharum*. These results indicate that single organs of some plants exhibit a high degree of reliability when extensive micromeasurements are used to detect genetic affinities.

KEY WORDS: Sugar Maple, *Acer saccharum*, Oklahoma, Numerical Taxonomy, Principal Coordinates, Relicts

Two isolated groups of sugar maples (*Acer saccharum* Marshall subsp. *saccharum*) occur in the prairies of west central Oklahoma approximately 320 km west of the edge of the continuous range of the eastern representatives of the species (Fig. 1). The nearest western relatives of these plants (*Acer saccharum* Marshall subsp. *grandidentatum* (Torrey and Gray) Desmarais (sensu lato)) occur ca. 480 km west in the Monzano Mountains of New Mexico and ca. 680 km southwest in the Edwards Plateau of Texas. The isolated Oklahoma populations are found in protected places in most of the canyons of the Caddo Canyons, Caddo and Canadian Counties, and approximately 80 km south in similar habitats in deep, sheltered canyons

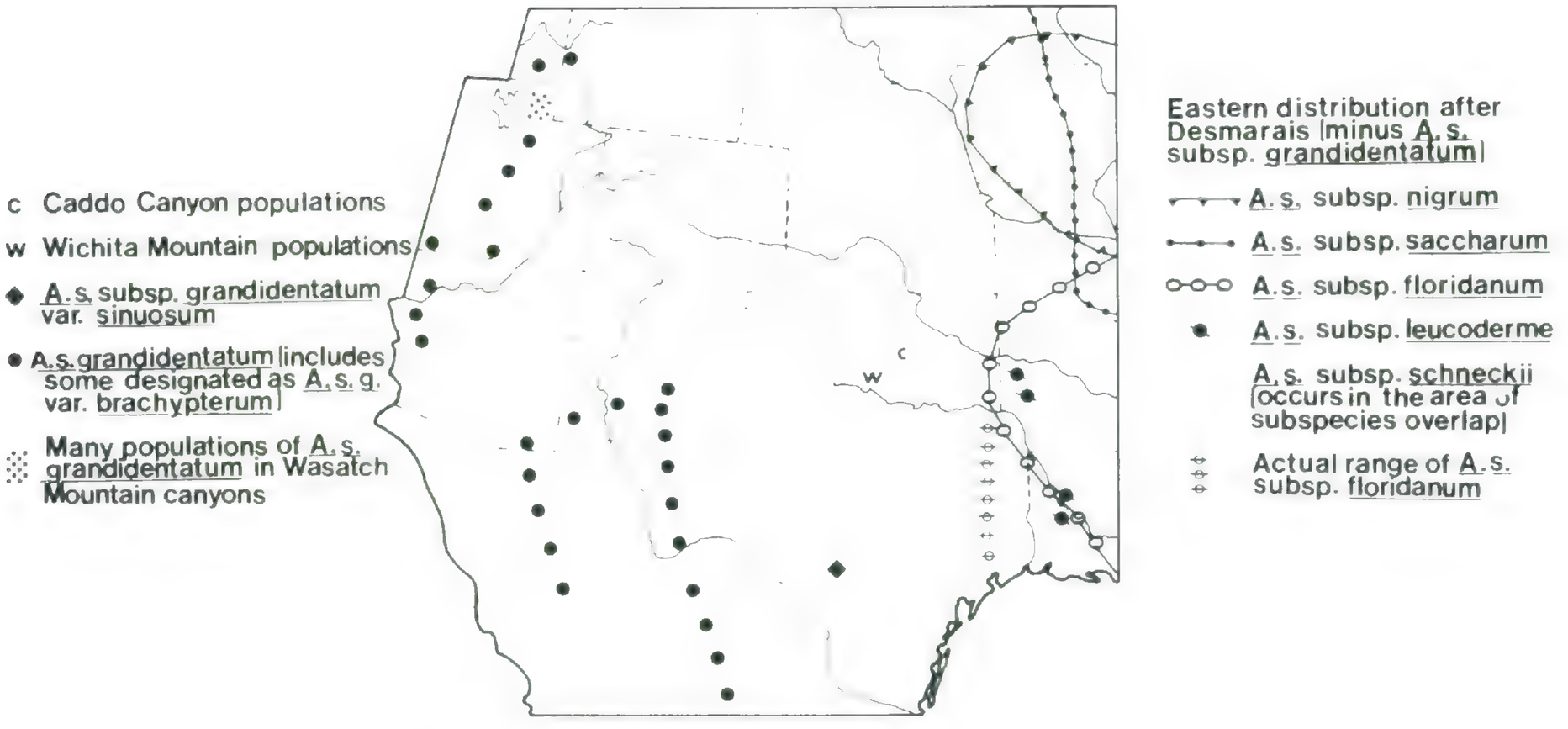

c Caddo Canyon populations
w Wichita Mountain populations
A.s. subsp. grandidentatum var. sinuosum
A.s. grandidentatum (includes some designated as A.s. g. var. brachypterum)
Many populations of A.s. grandidentatum in Wasatch Mountain canyons
c
w
Eastern distribution after Desmarais (minus A.s. subsp. grandidentatum)
A.s. subsp. nigrum
A.s. subsp. saccharum
A.s. subsp. floridanum
A.s. subsp. leucoderme
A.s. subsp. schneckii (occurs in the area of subspecies overlap)
Actual range of A.s. subsp. floridanum

Fig. 1. Distribution of sugar maple within which study sampling areas are located. Eastern ranges are after Desmarais (1952) except as noted. Oklahoma, western and Mexican locations are from population samples and herbarium records.

and north facing draws of the Wichita Mountains of Comanche County.

The Caddo Canyon plants have always been designated as subsp. *saccharum*. The populations of the Wichita Mountains were first assigned to *A. grandidentatum* Nuttall by Sargent (1922) with citation from an unpublished thesis by Stevens (1916). This represented a change from his inclusion of these plants as *A. saccharum* Marshall in the earlier 1905 edition of the Manual of Trees of North America. This idea of the more southern Oklahoma plants having western affinities was supported by Palmer (1934) who based his decision on the close field similarity of the plants of the Wichita stations to those in western locations. Little (1939, 1944) reinforced this interpretation. Hopkins (1943), however, recognized both groups as *A. saccharum*. He suggested that the plants of the Wichitas were ecological variants of the eastern species. Recent referrals agree with Hopkins' interpretation (Buck, 1964; Rice, 1960; Risser et al 1977), an exception being the work of Gehlbach and Gardner (1983).

The present investigation used a principal coordinates analysis of micromeasurements of leaf samples from 160 populations collected in the four major geographical areas involved; eastern and western United States and the Caddo Canyons and Wichita Mountains. This statistical procedure has resulted in a more objective conclusion about the relationship of the two groups to each other and their eastern and western relatives.

Methods

Measurements were based on Anderson and Hubricht's (1938) average leaf technique (Fig. 2). Raw measurement data[1] from selected populations from those studies were used directly for part of the eastern reference group. A second set of populations was taken from samples which had been pooled with the Anderson and Hubricht materials from studies done by Dansereau and Lafond (1941), Dansereau and Desmarais (1947), and Desmarias (1952). Pubescence

[1]See end of Appendix for availability of all raw measurement data for all populations included in this study.

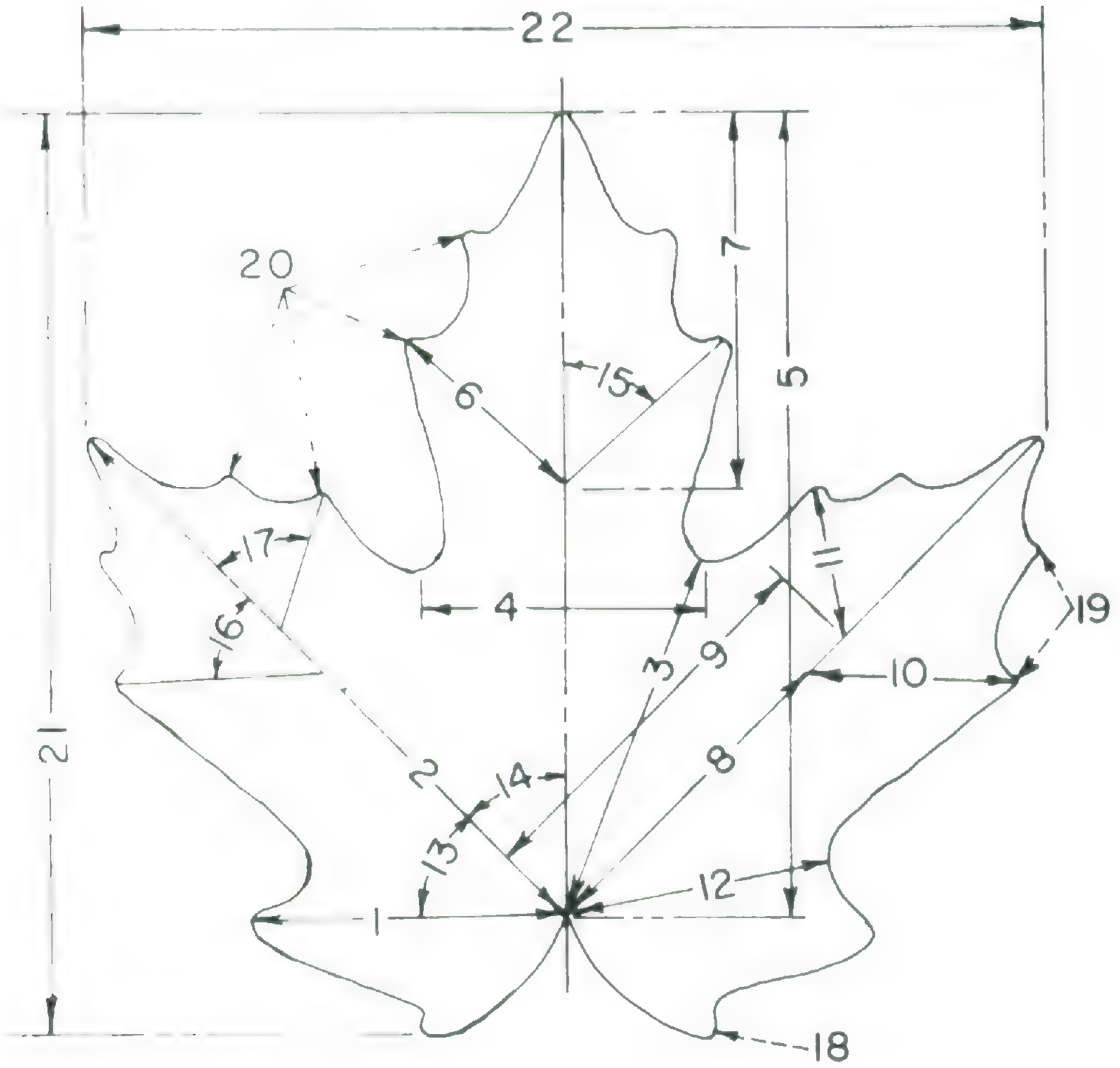


Fig. 2. Key to leaf measurements (Anderson and Hubricht, 1938).

scoring data were used directly from these studies but linear and angular measurements and lobe counts (1 22, Fig. 2) had to be taken because a subjective leaf shape coding technique had been substituted for these characters. These measurements, along with those for several new station additions, yielded an eastern reference of 50 populations (Appendix). Most of the populations used were selected from stations at the western edge of the range of the eastern groups so that they were located nearest to the Oklahoma isolates. They were for the most part those which Desmarais (1952) had coded as pure stands of *Acer saccharum* Marshall subsp. *saccharum*, subsp. *nigrum* (Michaux f.) Desmarais, subsp. *floridanum*

(Chapman) Desmarais, and subsp. *schneckii* (Rehder) Desmarais. Desmarais had only one small part of one collection designated as subsp. *leucoderme* (Small) Desmarais and no other populations were visited so this sole subspecies apparently was not represented in the numerical analysis of any study.

For populations from Oklahoma, southwestern United States, and an extensive western United States reference (Appendix), the sampling technique of Anderson and Hubricht (1938), which had also been employed by Desmarais et al, was utilized. Leaves were selected from 20 to 50 individuals but in some situations stand size restrictions yielded smaller representations. The population was inspected for a visual impression of a standard size and shape, majority leaf. One leaf was then subjectively chosen from each tree, from sterile stems, with at least two years growth and in semi-shade. An attempt was made to select the leaf at shoulder height where possible and atypical growth such as base sprouts, which often exhibit unusually large and sometimes shape distorted leaves, were avoided. Leaves were press dried, numbered, and stored in newsprint.

Pubescence density, undersurface color, and stipule presence scoring (characters 20–26, Table 1) was done for the new populations sampled for this study with a standard binocular microscope. The photographs from Desmarais (1952) were used as references. Figures 3 and 4 represent a clearer scanning electron microscope perspective for the pubescence judgments. A new pubescence character evaluating the density of indumentum along the edges of leaf margins was recorded for all populations included in the study (character 27, Table 1). The Demarais (1952) density criteria were used to score the marginal hair presence as pubescent, intermediate, or glabrous.

For the statistical analyses, linear measurements were converted to ratios (Fig. 2 and Table 1) to avoid the effect of ecomorphic distortion which would result if only gross leaf size was considered. A selected number of populations was used as individual operational taxonomic units (OTUs). In seven situations a number of populations was combined to form examplar OTU blocks (Appendix 1).

Analysis of variance (ANOVA) was run for each of the 27 characters to obtain F ratios (Table 1) and weights for various combinations of populations. The similarity measure used was an F–1

Table 1. Characters, character state values and F-ratios used in the computation of similarity ratios. Weights are F-1.0, where F is from analysis of variance of seven reference sample sets: FL 1, floridanum 1 (159 leaves); FL 2, floridanum 2, (34); UT, Utah populations of grandidentatum (254); NIG, nigrum (111); SAC 1, saccharum 1 from border states (181); SAC 2, saccharum 2 from eastern U.S. (237); and SCH schneckii (197).F.05 = 2.11; F.01 = 2.82; df = 6 1168. See Fig. 2 for character definitions.

	Character	Character State Value	F-Ratio
1.	5/2[1] ratio	actual value	13.2
2.	5/1 ratio	actual value	35.0
3.	5/7 ratio	actual value	18.0
4.	7/6 ratio	actual value	28.2
5.	(2 9) 11 ratio	actual value	33.8
6.	(2 8) 10 ratio	actual value	33.8
7.	22 21 ratio	actual value	33.9
8.	3 12 ratio	actual value	24.9
9.	(2 3) (5 3) ratio	actual value	20.1
10.	(1-12)/(2 12) ratio	actual value	33.2
11.	(sin. angle 15 × length 6)/ (.5 × length 4) ratio	actual value	13.0
12.	angle 13	actual value	150.6
13.	angle 14	actual value	39.9
14.	angle 15	actual value	27.0
15.	angle 16	actual value	83.2
16.	angle 17	actual value	100.0
17.	lobe count 18	actual value	80.0
18.	lobe count 19	actual value	137.0
19.	lobe count 20	actual value	189.3
20.	petiole pubescence	(P)[2] 2,(I)1,(G)0	14.8
21.	lower epidermis main vein pubescence	(P)2,(I)1,(G)0	266.2
22.	lower epidermis general pubescence	(P)2,(I)1,(G)0	289.1
23.	lower epidermis main axil	(P)2,(I)1,(G)0	197.2
24.	pubescence type	(E)1,(I)2,(A)3,(O),0	227.6
25.	lower epidermis color	(Y)1,(G)2,(V)0	266.7
26.	stipule presence	(O)0,(S)1,(L)2	67.3
27.	marginal hairs	(P)2,(I)1,(G)0	139.1

[1]See Figure 2.

[2]Anderson and Hubricht (1938) designations: petiole, various lower epidermis, and marginal hair density (P=very pubescent, I=intermediate pubescence, G=glabrous); position of hairs relative to the lower epidermis (E=erect, A=appressed, I=intermediate, O=glabrous); color of lower epidermis (Y=yellow green, G=glaucous, V=green); nature of stipules (O=absent, S=stipules, L=leaf-like stipules). Also see Figures 3 and 4 for pubescence characteristics.

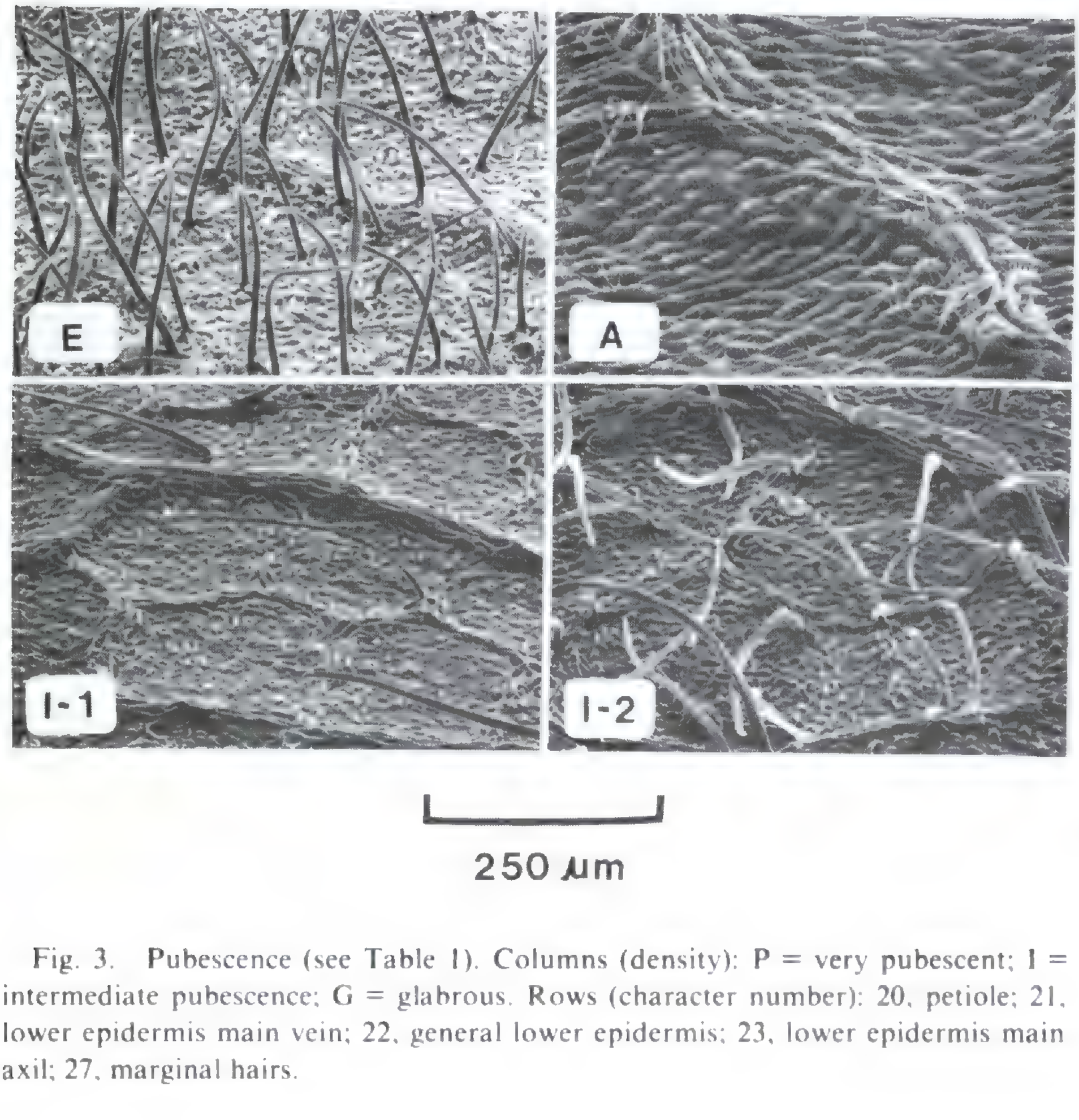


Fig. 3. Pubescence (see Table 1). Columns (density): P = very pubescent; I = intermediate pubescence; G = glabrous. Rows (character number): 20, petiole; 21, lower epidermis main vein; 22, general lower epidermis; 23, lower epidermis main axil; 27, marginal hairs.

weighted (F from ANOVA) mean character difference (MCD) as formulated by Adams (1975). Principal coordinate analyses (PCOORD) (Gower, 1966; Williams, Dale, and Lance, 1971) were performed using the similarity matrices for: 40 populations of *A. s.* subsp. *grandidentatum*; 18 populations of subsp. *saccharum* plus 6 populations of subsp. *nigrum*; and 20 populations of subsp. *floridanum* plus 14 populations of subsp. *schneckii*. From these PCOORD runs representative populations were chosen for use in constructing the examplars. It should be noted that PCOORD of the saccharum-nigrum populations revealed three distinct clusters and accordingly subsp. *saccharum* was divided into two examplars: SAC 1 and SAC 2. This was also the case for subsp. *floridanum* which was divided into FL 1 and FL 2. The population numbers included in the examplars are shown in the Appendix. This generated a set of F ratios

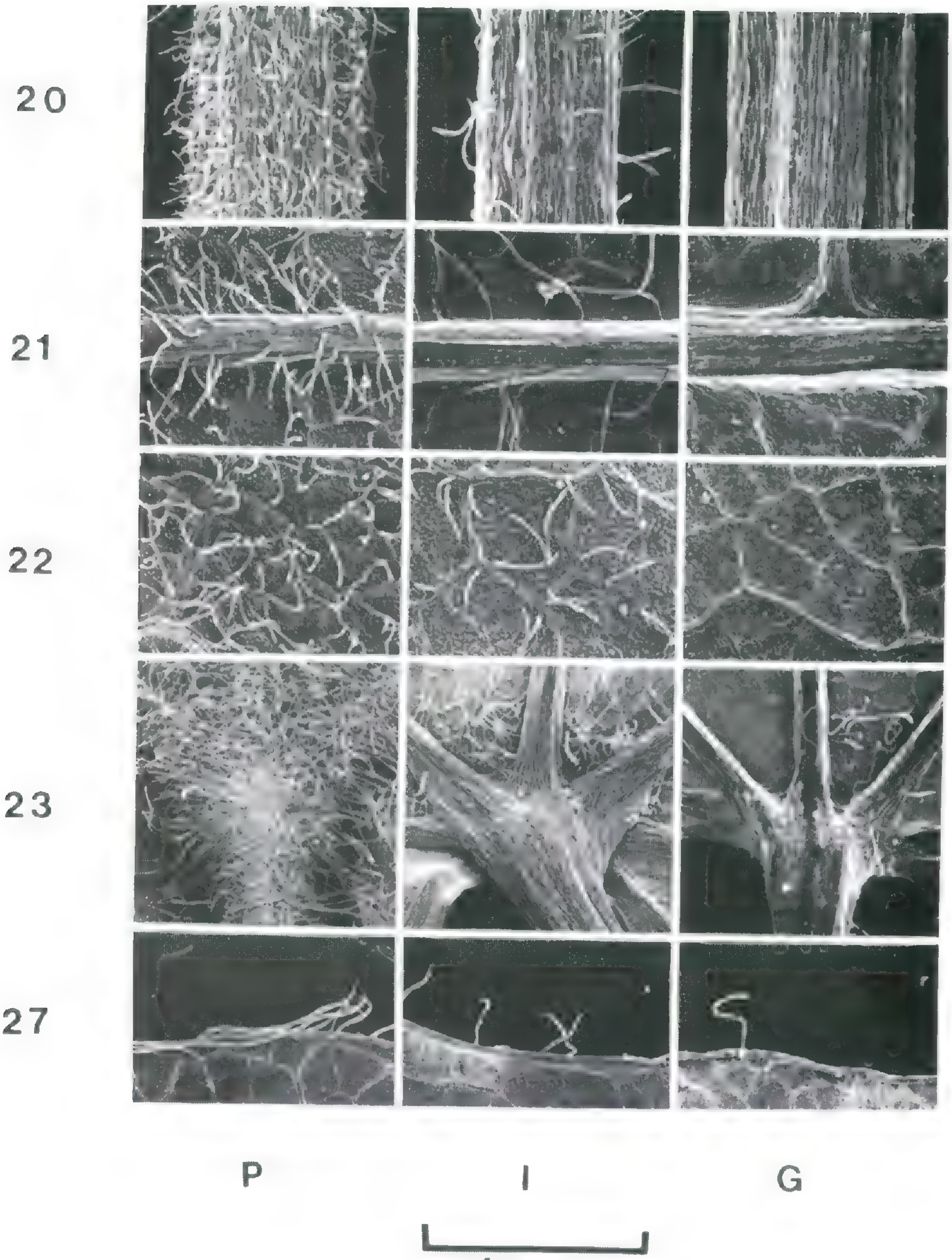


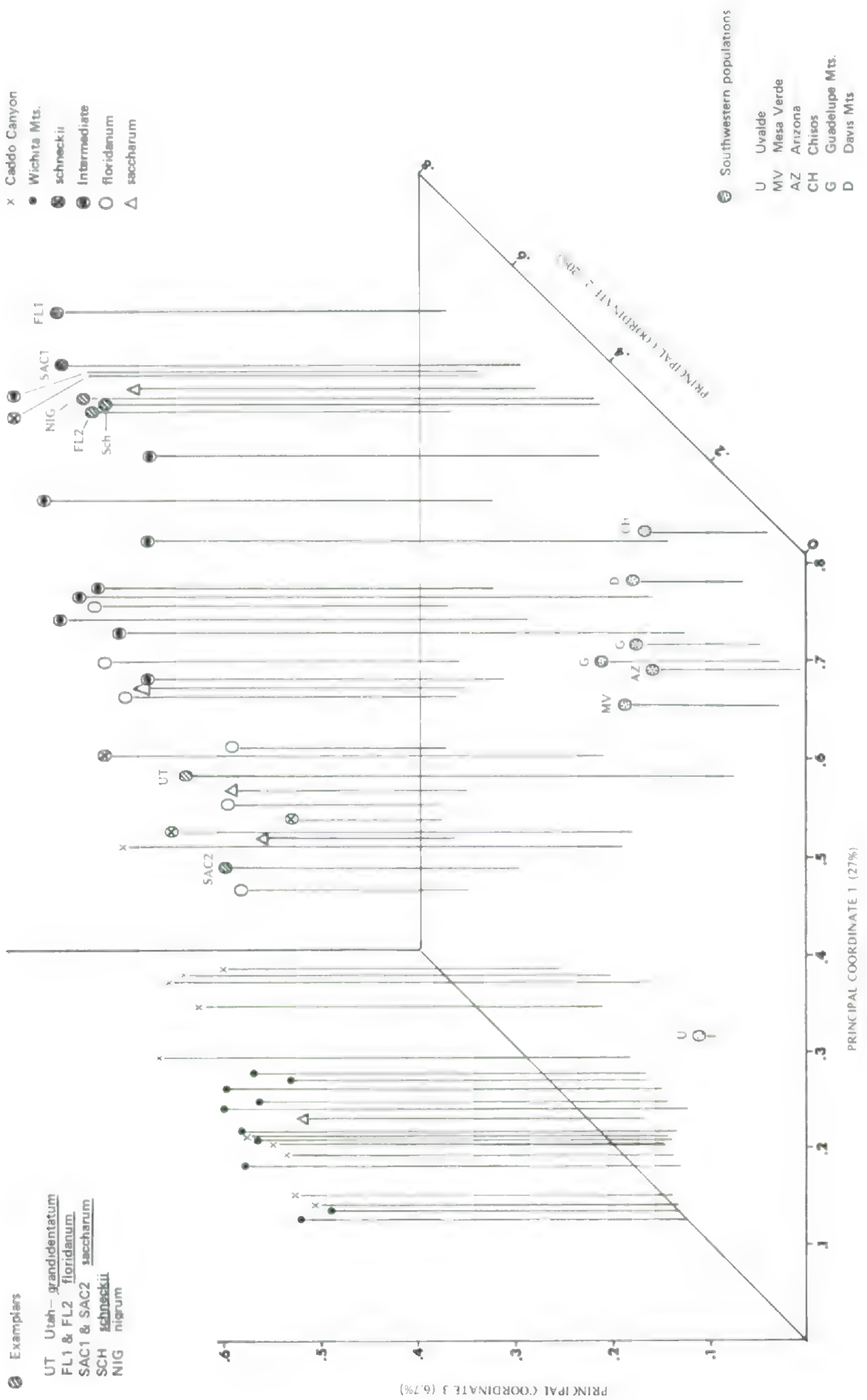
Fig. 4. Type of pubescence (see Table 1, character 24). E = erect; A = appressed; I-I = intermediate with most hairs in median position; I-2 = intermediate with approximately equal distribution of hairs in all positions.

(Table 1) which maximally discriminated between these seven examplars, 12 Caddo populations, 10 Wichita populations, 7 southwestern United States populations, and 25 border state eastern populations by using weights from ANOVA of the seven examplars. Principal coordinate analyses were then run on these 61 OTUs' similarity matrix to determine the affinities of the central Oklahoma populations to each other and to the western, southwestern and border state populations.

Six eigenroots were extracted (4.05, 2.92, 0.99, 0.82, 0.69, 0.52; Trace = 14.87) accounting for 67.3% of the variance. Each eigenroot explains a proportional amount of variation of the pattern among the OTUs. It is useful to represent these relationships in multidimensional space. Only the first three are presented here (Fig 5) as they appear to asymptote toward an error variance after the third root.

DISCUSSION

The ordination diagram of the first three principal coordinates (Fig. 5), reveals distinct separation of the four major geographical groups. The six southwestern populations (a fifth group) are also separated from the others. The western representatives (Examplar UT) align distinctly with the southwestern groups in the plane of PCOORD 1 and 2 but exhibits an interesting projection along axis 3. The two Oklahoma groups are indicated as more similar to each other than either is to the eastern and western references. The diagram also reveals a spatial orientation of the Oklahoma groups toward the eastern samples, especially in the plane of principal coordinates 1 and 2. In fact, one population from the Caddo Canyons and one from Rich Mountain, Arkansas fall within the boundary of the other. These placements, along with the strong field resemblance of the Caddo plants to eastern groups, is more persuasive that the populations of both Oklahoma stations are more recently influenced by the eastern gene pool. The decidedly strong subjective impression of the similar field morphology of the Wichita plants to western species is also outweighed by this statistical evidence.


× Caddo Canyon
• Wichita Mts.
schneckii
Intermediate
floridanum
saccharum
Southwestern populations
U Uvalde
MV Mesa Verde
AZ Arizona
CH Chisos
G Guadelupe Mts.
D Davis Mts
Examplars
UT Utah– grandidentatum
FL1 & FL2 floridanum
SAC1 & SAC2 saccharum
SCH schneckii
NIG nigrum
PRINCIPAL COORDINATE 1 (27%)
PRINCIPAL COORDINATE 2 (20%)
PRINCIPAL COORDINATE 3 (6.7%)

An earlier numerical analysis was made using the 80 populations referred to above from the east, 50 populations from the west and all of the samples from the Caddo Canyons and Wichita Mountains (Dent, 1969 a and b). A modification of the total difference index method of Russell (1964) was used. The results were similar to this current study but the more powerful PCOORD treatment presented here is considered more reliable.

The proposal of Little (1939, 1944) that the more southerly Wichita Mountain groups were more influenced by western subsp. *grandidentatum* germ plasm and the Caddo Canyon plants by eastern subsp. *saccharum* was not supported. This idea was originally presented based on subjectively perceived field similarities of the Wichita plants to western species (Palmer, 1934) and hypotheses of Sears (1932, 1933). Sears suggested that alternating mesic and xeric climates were induced in the interior plains by the irregular withdrawal of the Wisconsin ice sheet in the northern latitudes. Little's application proposed that the Oklahoma sugar maples represent arborescent survivor species of the two factions of a xerically separated but once continuous mid-continental east to the west distribution across the great plains. These flora were proposed to have approached within 80 km of each other during the last mesic (limited glacial advance) cycle. The southern vegetation tongue which terminated in the Wichita Mountains had developed western characteristics and the eastern derived fringe ended at the Caddo Canyons.

The final glacial retreat resulted in a return to a more xeric climate and the elimination of the more mesic-dependent species. The result over time was the establishment of the present, drier prairie flora. Sugar maple remained in more protected mesic sites as the only extant woody relict of this proposed migrational activity. All other species either persisted in a continuous range across the great plains (xeric tolerant) or were xerically terminated at the eastern edge of the prairies.

The mixture of eastern and western herbaceous flora found in both the Caddo Canyons and the Wichita Mountains indicated

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Fig. 5. Principal coordinate analysis. Note how the Caddo and Wichita populations cluster and the affinity of these to eastern populations. See Appendix for specific populations indicated by the key above.

some support for this interpretation (Hopkins, 1938 and 1943; Little, 1939; Rice, 1960) but the argument for a recent common association with the retreating mesic eastern flora for both west central Oklahoma sugar maple groups is more compelling. A recent study (Gehlbach and Gardner, 1983) which combined a similar numerical analysis with a flavonoid compound assessment concludes the opposite in favor of the Little designations and in addition assigns the Caddo plants to the hybrid status *A. s.* subsp. *floridanum* × *grandidentatum*.

The clustering indicated by the PCOOR ordination diagram (Fig. 5) reveals good separations for the major geographically identified groups (eastern, western-southwestern and Oklahoma). It does not present a clear picture for the traditional subspecies designations applied within the eastern United States range.

CONCLUSIONS

The principal coordinate evidence generated by this study indicated that the sugar maples of the Caddo Canyons and the Wichita Mountains of west central Oklahoma, while significantly isolated from each other and their eastern and western United States relatives, are more similar to each other than to outside reference populations, but are both more firmly aligned with eastern relatives. The eastern affinity hypothesis for both groups was reinforced by the few of those Caddo populations and the single western Arkansas representative which stray from their primary concentrations in the direction of the other. The best designation for all of the Oklahoma populations including the west-central isolates, is indicated to be the contemporary usage *Acer saccharum* Marshall subsp. *saccharum*. Use of the microanatomy of the leaf of these plants was a reliable statistical discriminator for large population groups but did not support the traditional sub-species designations for eastern United States.

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LITERATURE CITED

ADAMS, R. P. 1975. Statistical character weighting and similarity stability. Brittonia, **27**: 305–316.

ANDERSON, E., AND L. HUBRICHT. 1938. The American sugar maples. I. phylogenetic relationships, as deduced from a study of leaf variation. Bot. Gaz., **100**: 312–323.

BUCK, P. 1964. Relationships of the woody plants of the Wichita Mountains Wildlife Refuge to geological formations and soil types. Ecology, **45**: 336–344.

DANSEREAU, P. AND A. LAFOND, 1941. Introgression des characteres de l'*Acer saccharophorum* K. Koch et de l'*Acer nigrum* Michaux. Contr. Inst. Bot. Univ. Montreal, **37**: 15–31.

———., AND Y. DESMARAIS, 1947. Introgression in sugar maples II. Amer. Midland Naturalist, **37**: 146–161.

DENT, T. C. 1969a. Relationships of two isolated groups of sugar maple in central Oklahoma to eastern and western species. Dissertation: Ph.D., University of Oklahoma, Norman.

———. 1969b. 10PB chromosome number reports. Taxon **18**: 433.

DESMARAIS, Y. 1952. Dynamics of leaf variation in the sugar maples. Brittonia, 7: 347–387.

GEHLBACH, F. R. AND R. C. GARDNER, 1983. Relationships of sugar maples (*Acer saccharum* and *A. grandidentatum*) in Texas and Oklahoma with special reference to relict populations. Texas Journ. Sci. **35**: 231–237.

GOWER, J. C. 1966. Some distance properties of latent root vector methods used in multivariate analysis. Biometrika, **53**: 325–338.

HOPKINS, M. 1938. Notes from the University of Oklahoma Herbarium. Rhodora, **40**: 431–434.

———. 1943. Notes from the Bebb Herbarium. Rhodora, **45**: 273–275.

LITTLE, E. L. JR. 1939. The vegetation of the Caddo County canyons, Oklahoma. Ecology, **20**: 1–10.

———. 1944. *Acer grandidentatum* in Oklahoma. Rhodora **40**: 445–450.

PALMER, E. J. 1934. Notes on some plants of Oklahoma. J. Arnold Arb., **15**: 127–134.

RICE, E. L. 1960. The microclimate of a relict stand of sugar maple in Devil's Canyon in Canadian County, Oklahoma. Ecology, **41**: 445–453.

RISSER, P. G., G. D. SCHNELL, AND J. F. HELSEL. 1977. Factor analysis of tree distribution patterns in Oklahoma. Ecology, **58**: 1345–1355.

RUSSELL, N. H. 1964. Quantitative studies in angiosperm taxonomy. X. *Valeriana*. XI. *Geranium*. XII. *Mimulus*. Castanea, **29**: 138–150.

SARGENT, C. S. 1922. Manual of the Trees of North America. Houghton, Mifflin and Co. NY.

SEARS, P. B. 1932. The archeology of environment in North America. Amer. Anthr., **34**: 610–622.

———. 1933. Climate changes as a factor in forest succession. J. For., **31**: 934–942.

STEVENS, G. W. 1916. The flora of Oklahoma. Dissertation: Ph.D., Harvard University, Cambridge, MA.

WILLIAMS, W. T., M. B. DALE, AND G. N. LANCE. 1971. Two outstanding ordination problems. Aust. J. Bot., **19**: 251–258.

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS

POPULATION NO.[1]	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
CADDO CANYONS (12 populations)					491
1	OK	Caddo	Red Rock Canyon	35	
2	OK	Caddo	Devil's Canyon, Pioneer Camp #2	34	
3	OK	Canadian	Devil's Canyon Widder Maker	44	
4	OK	Canadian	Devil's Canyon Methodist Campground	53	
11	OK	Caddo	Salyor Lake	57	
12	OK	Caddo	Wildcat Creek	57	
71	OK	Canadian	Upper Kickapoo Creek	26	
72	OK	Canadian	Kickapoo Valley	36	
73	OK	Caddo	Medicine Creek	36	
74	OK	Canadian	Water Canyon	44	
163	OK	Caddo	Red Rock State Park Main Canyon	27	
164	OK	Caddo	Devil's Canyon Pioneer Camp	42	
WICHITA MOUNTAINS (10 populations, Wichita Wildlife Refuge)					495
5	OK	Comanche	Hollis Canyon	60	
6	OK	Comanche	Mount Pinchot	53	
7	OK	Comanche	Baker Peak No. 1	60	
8	OK	Comanche	Baker Peak No. 2	40	
9	OK	Comanche	Panther Creek	42	
10	OK	Comanche	Greenleaf Canyon	41	
13	OK	Comanche	Boulder Camp	57	
77	OK	Comanche	Halley Canyon	42	
162	OK	Comanche	Mount Scott	40	
178	OK	Comanche	Elk Mountain	60	

[1]Numbers assigned by Dent for new population samples and to those used from previous studies.

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS (continued)

POPULATION NO.[1]	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
TEXAS-SOUTHWEST (7 populations)					277
14	TX	Bandera	Vanderpool Warren Murphy Ranch	42	
15	TX	Brewster	Big Bend N.P. Boot Springs	52	
16	TX	Jeff Davis	Toyahville Little Ajuga Canyon	45	
17	TX	Culberson	McKittrick Canyon	48	
20	CO	Montezuma	Mesa Verde	46	
130*	AZ	Cochise	Coronado N.F. Oak Creek Canyon	10	
168	TX	Culberson	Pine Springs	34	
Border STATES (25 populations)					972
saccharum					197
144*	AR	Benton	Gateway	35	
145*	AR	Crawford	Chester Kimes Mountains	44	
154*	MO	Camden	Tunnel Dam	55	
179	AR	Polk	Rich Mountain No. 1	38	
180	OK	McCurtain	Idabell Little River	25	
schneckii					120
90*	MO	Christain	Highlandville	25	
91*	MO	Texas	Clear Spring	21	
93*	MO	Pulaski	Big Pines River	15	
137*	MO	Taney	Hollister Lake Taneycomo	28	
138*	MO	Texas	Jacks Fork River	31	
floridanum					253
121*	AR	Scott	Boles Big Forche River	44	
122*	AR	Benton	Rogers Devil's Eyebrow	43	
124*	AR	Crawford	Chester Sugar Camp	43	
128*	AR	Carroll	Eureka Springs King's Springs	43	
135*	AR	Carroll	Eureka Springs	43	
136*	AR	Polk	Rich Mountain No. 2	37	

*Population samples from previous studies

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS (continued)

POPULATION NO.[1]	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
intermediate					402
101*	IL	Effingham	Hill	46	
102*	MO	Lewis	Canton	26	
103*	IL	Lee	Dixon	46	
104*	IL	Ogle	Byron	48	
105*	IL	Henry	Cambridge	45	
132*	MI	Kalamazoo	Schoolcraft Nesbit Corners	50	
133*	MO	Dent	Montauk S.P.	52	
134*	MO	Morgan	Gravois Mills Gravois Springs	56	
142*	MO	Callaway	New Bloomfield Hiller Creek	33	
EXAMPLARS (30 populations)					1173
grandidentatum (UT)					254
28	UT	Utah	Alpine Fort Canyon	49	
48	UT	Wasatch	Deer Creek Reservoir Hanks Canyon	58	
51	UT	Utah	Timpagnogos Campground American Fork Canyon	51	
55	UT	Wasatch	Midway Snake Creek Canyon	50	
68	UT	Cache	Mendon Maple Bench	46	
saccharum (SAC 1, pure border states)					181
84*	IL	Tazewell	Peoria	50	
146*	IA	Jones	Wapsipinicon S.P.	21	
149*	MN	Scott	Spring Lake	23	
150*	MN	Benton	Foley	45	
153*	MO	Marion	Hannibal MarkTwain Cave	42	
saccharum (SAC 2, pure miscellaneous eastern)					237
79	WV	Grant	Mount Storm Edgewood Farm	47	
156*	MA	Worcester	Petersham	60	
165	OH	Geauga	Chardon Bass Lake Sugar Camp	46	
166	WV	Preston	Cranesville Fenston Farm	60	
167	OH	Medina	Cleveland M.P.S. Hinkley Ridge	24	

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS (continued)

POPULATION NO.[1]	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
nigrum (NIG)					111
82*	IA	Lee	Montrose	31	
85*	IA	Kossuth	Algona	50	
86*	IA	Kossuth	Algona	30	
schneckii (SCH)					197
87*	IL	Monroe	Fountain Gap	60	
88*	MO	Franklin	Fiddle Creek	45	
95*	MO	St. Francis	Koester	27	
96*	MO	St. Lewis	Eureka Rankin Estate	42	
139*	MO	Franklin	Robertsville Meramec River	23	
floridanum (FL 1, Crowley's Ridge)					159
123*	AR	St. Francis	Forest City	44	
125*	AR	Phillips	Helena	29	
126*	AR	Green	Paragould	43	
127*	AR	Phillips	Helena	43	
floridanum (FL 2)					34
106*	GA	Bartow	Emerson	12	
107*	GA	Cobb	Bolton	16	
108*	GA	Clarke	Whitehall	6	
TOTAL LEAVES IN STUDY					3408

NOTES: FIELD COLLECTION SITE LOCATIONS AND RAW DATA MEASUREMENT AVAILABILITY FOR ALL POPULATION SAMPLE SPECIMENS COLLECTED FOR THIS AND ALL OTHER STUDIES (ALL SPECIMENS CURRENTLY HOUSED AT LAVAL UNIVERSITY, QUEBEC, CANADA) Complete location information regarding collection sites and tables of all measurement data for this and all previous projects are available as follows. Portions of the senior author's field log are also available by direct request.

1. ADI Auxiliary Publications Project

Photoduplicating Service, Library of Congress, Washington, D.C. 20540.
ADI Document No. 3577 "Dynamics of Leaf Variation in Sugar Maples". Pooled collections from previous studies (Desmarais, 1952). Microfilm $7.23. Photocopies $21.30.

2. Microfiche Publications.

A. See NAPS Document No. 03410 for 520 pages of supplementary material. "Relationships of West Central Oklahoma Sugar Maples to Eastern and Western Species". Dent collections (1963-68) plus populations selected from Desmarais' pooled collections.

Order from NAPS c/o Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, NY 10017. Remit in advance in U.S. funds only $130.00 for photocopies or $3.00 for microfiche. Outside the U.S. and Canada add postage of $3.00 for photocopy and $1.00 for microfiche.

B. See NAPS Document No. 03411 for 77 pages of SUPPLEMENTARY material. "Relationships of West Central Oklahoma Sugar Maples to Eastern and Western Species". Dent collections (1963-68) plus populations selected from Desmarais pooled collections. Collection locations, character averages and standard deviations—individual leaf measurements omitted. Order from NAPS as listed above. Remit in U.S. funds only $19.25 for photocopies or $3.00 for microfiche.

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A NOTE ON THE GROWTH HABIT OF FRINGED POLYGALA

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ABSTRACT

The green leaves and flowers of *Polygala paucifolia* occur along the terminal, upright portions of long thin rhizomes that grow out from a small perennial tuber. Each tuber sends out several new rhizomes annually. New tubers are produced at the scale leaf nodes of the horizontal portion of the rhizome through the multiplication of lateral buds and through secondary vascular growth. This mode of vegetative reproduction increases the longevity of a plant and spreads an individual laterally.

In this paper I describe the vegetative growth of *Polygala paucifolia* Willd. (Polygalaceae) emphasizing the development of the perennial, subterranean organs. Although these small tuberous structures are often included in herbarium material of *P. paucifolia*, a description of their ontogeny and role in the life history of the species is absent from systematic treatments of the genus (Wheelock, 1891; Miller, 1971).

There is little recent literature on the morphology and anatomy of the genus. Holm (1929) mentions the existence of what he inappropriately calls a "pseudo-rhizome", but he was unaware of its curious development. The following account is based on material excavated on several occasions during 1982 from natural populations growing in Harvard Forest, Petersham, Massachusetts, and from an oak woods near Bellows Falls, Vermont. I confirmed certain phenological observations by making repeat visits to marked plants. A survey of the herbaria of Harvard University and the New England Botanical Club failed to show any significant geographic variation in growth habit.

Polygala paucifolia blooms in Massachusetts during the latter part of May and the first two weeks of June, often forming conspicuous patches on the forest floor. A short vegetative axis, usually with basal cleistogamous flowers, supports 3-7 photosynthetic leaves and frequently terminates with a pair of chasmogamous flowers. Careful excavation reveals that this upright shoot is the end of a pale, thin (1.0-1.5 mm diameter) horizontal stem, resting 1–2 cm beneath the soil litter. This stem can be traced back 5–30 cm to a small (1–5 mm diameter), well rooted, tuberous organ from which several other horizontal stems radiate.

Along this horizontal stem occur scale leaves arranged in a spiral fashion, with internodes ranging from one to seven centimeters. Each scale leaf subtends an axillary bud that may be in one of four conditions: (1) inactive, (2) growing as a horizontal shoot, the parent axis then being branched, (3) growing as a short vertical vegetative shoot, (4) growing as a short vertical shoot terminating in a pair of cleistogamous flowers. Typically, the cleistogamous flowers are found on a lateral appendage near the base of the chasmogamous flowering stem. All four conditions are represented in Figure 1a.

A tuber is the source of the horizontal stems, but the critical feature of the growth habit is that the horizontal stems are a source of new tubers. These tubers develop at the scale leaf nodes over the course of several years, and three processes are involved: root initiation, meristem proliferation, and secondary vascular growth. The following account describes a typcial course of tuber development.

When a lateral bud grows out, one or two adventitious roots are initiated on the new stem immediately adjacent to the parent axis (Fig. 1b). There are no roots on the parent stem and no further roots will form at this node. Immediately above the adventitious roots, a pair of scale leaves and axillary buds are initiated, followed by a long internode separating them from subsequently formed photosynthetic leaves. The lateral shoot that bears these structures will live through the summer, fall, and possibly winter before dying back to a point just above the scale leaves. The buds in the axils of those scale leaves then grow out, and each in turn will form its own pair of basal scale leaves and axillary buds (Fig. 1c). Note that the plane of bud insertion is always perpendicular to that of the previous year. This process of shoot die back and basal bud proliferation is repeated annually and leads to a tuber (at this stage, really a condense sympodial branch system) with an increasing number of meristems (Fig. 1d). About the third year in its development, the tuber becomes independent of the parent axis which decays at the adjacent internodes. Continued meristem proliferation and secondary vascular growth in both roots and stems (Fig. 1e) leads to a mature tuber (Fig. 1f).

The tuber contributes toward the longevity of the individual by its own survival and through the potential it provides for the development of new tubers on the annual crop of runners. This growth

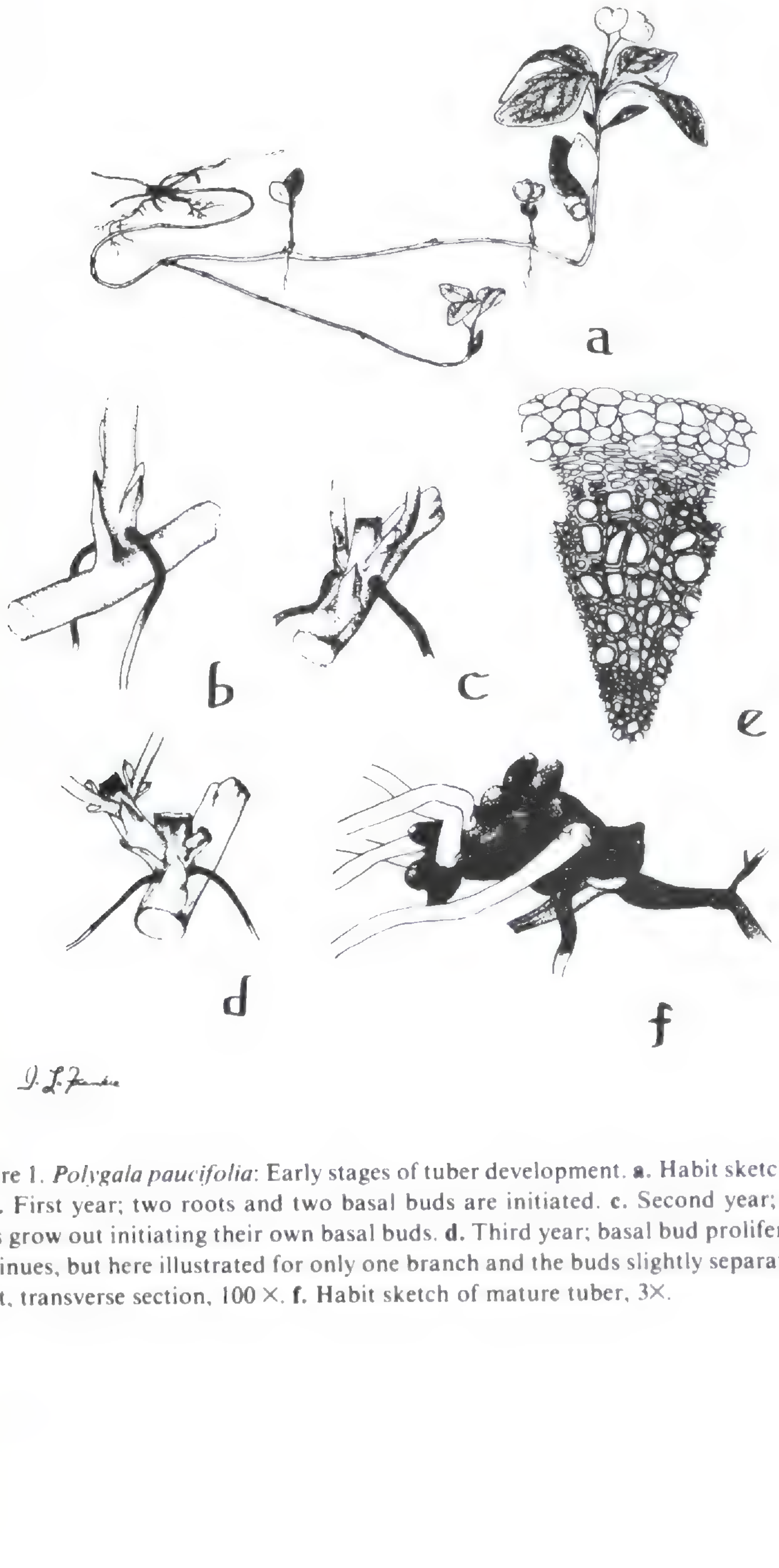

Figure 1. *Polygala paucifolia*: Early stages of tuber development. **a.** Habit sketch, 1/3 ×. **b.** First year; two roots and two basal buds are initiated. **c.** Second year; basal buds grow out initiating their own basal buds. **d.** Third year; basal bud proliferation continues, but here illustrated for only one branch and the buds slightly separated. **e.** Root, transverse section, 100 ×. **f.** Habit sketch of mature tuber, 3×.

habit has the added advantage of allowing for the lateral spread of a plant. The longevity of individual tubers is uncertain, though their importance in proliferation and perennation seems obvious. This provides a clue as to how certain unique populations of blue and white flowered plants have persisted in particular locations for over 75 years (Eaton, 1952).

LITERATURE CITED

EATON, R. J. 1952. Persistence of color forms of *Polygala paucifolia*. Rhodora **4**: 27-28.

HOLM, T. 1929. Morphology of North American species of *Polygala*. Botanical Gazette **88**: 167-185.

MILLER, N. G. 1971. The Polygalaceae in the Southeastern United States. Journal of the Arnold Arboretum **52**: 267-284.

WHEELOCK, W. E. 1891. The genus *Polygala* in North America. Memoirs of the Torrey Botanical Club **2**: 109-152.

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DISCOID HEADS: AN INHERITABLE TRAIT IN *CHRYSANTHEMUM LEUCANTHEMUM* L.

A. Linn Bogle

In the spring of 1976, a plant of *Chrysanthemum leucanthemum* L., Ox-eyed daisy, was found growing on disturbed ground in Durham, New Hampshire. This was a robust plant with numerous heads, all of which lacked the normal white ray florets and consisted only of yellow disc florets. Many other plants of this species growing in the same disturbed area were all normal, with numerous white ray florets in each head.

The heads of the anomalous plant were all mature or nearly so, and a few had shattered and shed their seed. The heads had presumably been open-pollinated with numerous surrounding normal radiate plants. A search of the entire area turned up no other rayless plants. During the search, however, a few heads were discovered that appeared rayless or partially so at first glance, but closer examination revealed that the white rays had been harvested by some foraging insect, perhaps as food. Haber (1980) reports such foraging on the disc and ray florets of the Flat-topped white aster, *Aster umbellatus*, by the Broad-winged Bush-katydid, *Scudderia pistillata*, near Ottawa, Ontario, Canada. I have not yet been able to find an insect in the act of foraging, despite searches through various populations of flowering *C. leucanthemum* showing evidence of such activity.

Notes in some taxonomic descriptions of *Chrysanthemum leucanthemum* indicate that a condition such as this may have been noted previously. *Gray's Manual* (Fernald, 1950) notes parenthetically that rays may be "rarely tubular, laciniate or deformed" for the typical variety, and that a "Forma *tubuliflorum* Hendrikssen (tubular-flowered) has tubular ligules" under var. *pinnatifidum* Lecoq. & Lamotte. Similarly, in the *Flora Europeae*, Heywood (1976, as *Leucanthemum vulgare* Lam.) notes that ligules may be "rarely very short or absent." Self-incompatability or slight self-compatability is noted for a number of species of *Chrysanthemum* by Fryxell (1957), but I have found no references to indicate

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research on the breeding system or inheritance of discoidy in the species, or that hybridization between naturally occurring discoid and radiate types may have given rise to plants with short rays, such as those noted by Heywood. Some closely related species of *Chrysanthemum* such as *C. Balsamita* L., or related genera, such as *Tanacetum* L., have both radiate and discoid forms, or show varying degrees of ray reduction.

A similar genetically controlled discoid condition in normally radiate taxa has been demonstrated in such genera as *Bidens pilosa* L., tribe Heliantheae (Rajan, 1977); *Senecio vulgaris* L. and *S. squalidus* L., tribe Senecioneae (Ingram & Taylor, 1982); and *Layia glandulosa* (Hook.) H. &. A. (Clausen, Keck, & Heisey, 1947), tribe Heliantheae, among others (see Burtt, 1977). In these genera it has been shown that hybridization between normal radiate plants and spontaneous mutant discoid plants have given rise to hybrid intermediates that bridge the gap between the two extreme forms. This has not been shown to have occurred, as yet, in *Chrysanthemum leucanthemum*.

To determine whether the discoid condition was a heritable trait, and to develop a population of plants for experimental work, seed from the original plant were germinated in the University of New Hampshire greenhouses. Of 120 second generation progeny recovered, two eventually proved to be discoid. The first progeny began to flower in the late spring of 1978. Of these, one plant was discoid, bearing a single head, the other plants were radiate. At the time of the discovery, three or four rows of peripheral florets had opened in its discoid head and were subject to open pollination with nearby radiate siblings by random insect visitors having access to the greenhouse through the ventilation louvres. The plant was isolated in a screen enclosed pollination cage that excluded any pollinators, so that the more central florets were presumably selfed. However, it was not possible to distinguish among the seeds when they were harvested. The second discoid plant bloomed in 1981. The last second generation plant bloomed in 1983. None of the second generation radiate plants showed obvious reduction in the number of ray florets or in ray length.

Seeds harvested from the first discoid head in the second generation produced 62 third generation progeny which were maintained in the greenhouse. Of these, 31 proved to be radiate and 27 discoid

(four died without flowering). As in the second generation, none of the radiate progeny exhibited any obvious reduction in the number of ray florets, or in the length of the ligule in ray florets, such as that resulting from hybridization between normal radiate and mutant discoid heads in *Bidens*, *Layia*, or *Senecio*. This may indicate that no cross-pollination took place between discoid and radiate siblings, or that a different genetic mechanism is in effect from that in the other genera cited.

Most of the second and third generation plants were not significantly different in appearance from naturally occurring plants, but a few of the third generation plants had a striking columnar growth habit rather than the more typical sessile rosetted form. At the tip of a thick central axis up to 15 cm. long and 2 cm. thick they bore a terminal rosette of dark green leaves with darkly anthocyanous petioles which were reflexed at their bases, so that the leaves bent downward. The general appearance was that of a miniature "tree" composite.

Based on visual inspection alone leaf form among the third generation progeny is obviously variable. Most of the plants resemble var. *pinnatifidium* (var. *subpinnatifidum* of Fernald, 1903), although a few tend toward the typical variety. However, leaf form is too variable to allow attribution of all the plants to one variety or the other. In addition, chromosome counts of $2n = 18$ were found in one radiate and one discoid plant of the third generation. Mulligan (1958) found var. *pinnatifidum* (as var. *subpinnatifidum*) to be diploid, with $2n = 18$, and var. *leucanthemum* to be tetraploid, with $2n = 36$. In this respect, the leaf form of the large majority of third generation plants would correspond with Mulligan's observations on the correlation of leaf form and chromosome number.

There is some indication that flowering time can differ, at least in the greenhouse, between the discoid and radiate siblings. The seeds from the second generation discoid plant were planted in the summer of 1978. The first three third generation plants to bloom in 1980 were discoid, with the discoid plants tending to flower earlier than the radiate siblings. In the late winter and spring of 1982-83, the discoid plants began to flower in late January and February, and practically all were in flower before the first of the radiate siblings began to flower. Both types then continued to flower through much of the summer, well beyond the normal flowering period in the field.

The recognition of the occurrence and inheritance of discoidy in *Chrysanthemum leucanthemum* may lead to a better understanding of some of the variation in the species. Seeds resulting from open- and self-pollinated third generation discoid and radiate plants are being grown to check variation in the fourth generation.

LITERATURE CITED

Burtt, B. L. 1977. Aspects of diversification in the capitulum. Pp. 41-59 *in*: V. H. Heywood, J. B. Harbourne, & B. L. Turner (eds.), The Biology and Chemistry of the Compositae. Academic Press, London.

Clausen, J., D. D. Keck & W. H. Heisey. 1947. Heredity of Geographically and Ecologically Isolated Races. Amer. Naturalist. **81**: 114-133.

Fernald, M. L. 1903. *Chrysanthemum leucanthemum* and the American white weed. Rhodora. **5**: 177-181.

_____ 1950. Gray's Manual of Botany, 8th Ed. American Book Co. New York.

Fryxell, P. A. 1957. Modes of reproduction in higher plants. Bot. Rev. **23**: 135-233.

Haber, E. 1980. Aster Florets in the Diet of Broad-winged Bush-katydid. Canad. Field-Naturalist. **94**: 194-195.

Heywood, V. H. 1976. *Leucanthemum* Miller. Pp. 174-177 *in*: T. G. Tutin, et al. (eds.). Flora Europaea. Vol. 4. Cambridge Univ. Press, Cambridge.

Ingram, R., & L. Taylor. 1982. The Genetic Control of a Non-radiate Condition in *Senecio squalidus* L. and Some Observations on the Role of Ray Florets in the Compositae. New Phytologist. **91**: 749-756.

Mulligan, G. A. 1958. Chromosome races in the *Chrysanthemum leucanthemum* complex. Rhodora **60**: 122-125.

Rajan, S. S. 1977. Ray Reduction in Flowers and Evolution in *Bidens pilosa* Linn. New Botanist **IV** (1-4): 95-98.

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